

FOSSIL BOVIDAE (MAMMALIA) FROM LANGEBAANWEG, SOUTH AFRICA

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(With 63 figures and 6 tables)

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ABSTRACT

Fossil Bovidae are described from the Quartzose Sand Member and Pelletal Phosphorite Member of the Varswater Formation in 'E' Quarry, Langebaanweg. The new genus *Damalacra* and the new species *Simatherium demissum*, *Kobus subdolos*, *Damalacra neanica*, *D. acalla* and *Raphicerus paralius* are named. The bovids best fit a very late Miocene age of about 6 million years B.P. according to faunal correlations with other sites for some of which radiometric dates are available. Evidence from other mammalian groups present in 'E' Quarry may suggest alternative ages.

The Bovidae of Baard's Quarry, Langebaanweg, are also discussed. The lower assemblage is younger than the 'E' Quarry faunas, perhaps even of Pleistocene age; the upper assemblage is of Middle Pleistocene age or later.

CONTENTS

	PAGE
Introduction	214
Bovidae from 'E' Quarry	219
Tribe Tragelaphini	219
Tribe Boselaphini	224
Tribe Bovini	232
Tribe Reduncini	247
Tribe Alcelaphini	264
Tribe Neotragini	299
Tribe Antilopini	310
Tribe Oribovini	315
Enigmatic horn-cores	321
Bovidae from Baard's Quarry	321
Tribe Boselaphini	321
Tribe Reduncini	321
Tribe Hippotragini	324
Tribe Alcelaphini	324
Tribe Neotragini	325
Tribe Antilopini	326
Age of the Bovidae from Baard's Quarry	327
Discussion	328
Acknowledgements	333
References	334

INTRODUCTION

The late Tertiary fossil vertebrate site of Langebaanweg is situated 105 km north-north-west of Cape Town and about 15 km inland from Saldanha Bay at 32°58'S 18°09'E. Faunal and geological studies of the site have been made by Hendey (1970, 1973, 1974, 1976) and Tankard (1974). Commercial mining for phosphates led to the opening of a number of quarries in which Tertiary gravels, sands and clays were exposed beneath the covering of Pleistocene and Recent sands. Most of the abundant remains of freshwater, marine, terrestrial and flying vertebrates have come from deposits constituting the Varswater Formation in the New Varswater Mine or 'E' Quarry. A smaller number came from unnamed deposits in Baard's Quarry, but this has now been backfilled and the relationships of its deposits to those in 'E' Quarry are uncertain. All unqualified references to Langebaanweg fossils are to those from 'E' Quarry. 'E' Quarry is the type locality for the Varswater Formation, and its stratigraphy is as follows:

Largely or entirely Pleistocene/ Holocene	Surface bed
Latest Miocene/early Pliocene	Varswater Formation: Pelletal Phosphorite Member Quartzose Sand Member Gravel Member
Miocene	Saldanha Formation

The Varswater Formation is only about 10 m thick in 'E' Quarry, but elsewhere it can reach 39–43 m. Its deposition was initiated by a marine transgression probably in the late Miocene during which the Gravel Member was deposited in a rocky and sandy marine beach environment. This member consists of boulders, cobbles and pebbles of phosphate rock in sands and has yielded marine invertebrates and vertebrates. Terrestrial vertebrates are rarer and their bones have usually been heavily rolled, evidently the result of wave action.

There followed a stillstand in the transgression, during which the Quartzose Sand Member was accumulated in a variety of depositional environments in and near an estuary. Lithologically it is the most complex of the Varswater members in 'E' Quarry and the demarcation of its upper and lower limits has been difficult. Three main facies are recognized within the Quartzose Sand Member. The first, of which there are extensive exposures, is composed of largely non-phosphatic quartz sands, believed to represent a floodplain environment. This unit contains vertebrate fossils which accumulated both subaerially and subaqueously. The second is an horizon of carbonaceous sand and clay (the 'peat bed'), which probably represents a marsh environment. The third facies is a muddy silt rich in invertebrate fossils but without significant vertebrates, which apparently represents a tidal mudflats accumulation. Exposures of the marsh and tidal mudflats facies are limited in extent.

The final phase of the transgression was the period of accumulation of the Pelletal Phosphorite Member—medium grade phosphatic sands whose base truncates the Quartzose Sand Member. The lowermost part of it in 'E' Quarry was laid down in shallow marine water, and the remains of both terrestrial and aquatic vertebrates are numerous in restricted areas in, and immediately adjacent to, a river channel. It is believed that the course of the river shifted northward as the transgression progressed and two distinct channels have been exposed. These deposits are informally termed bed 3aS and bed 3aN (Hendey 1976: 226), the former being the older. The duration of the intervals between deposition of the Quartzose Sand Member and bed 3aS and between beds 3aS and 3aN are not known.

The mammal fauna from 'E' Quarry has been discussed by Hendey (1976: 231–243). The larger mammals of the Quartzose Sand Member are those on which the relative dating originally depended, and Hendey (1973: 13; 1974: 61, 62) inferred an age of about 4,5 m.y. by correlation with dated east African faunas. There is now more uncertainty about the age, and the Varswater Formation may have accumulated over an appreciable period. It is, however, generally agreed that none of the sediments is likely to be younger than 3,5 m.y. and none older than about 7 m.y. (Hendey 1978*b*: 267–269). The varied herbivores suggest a more luxuriant vegetation than exists in the area at the present time, and there is evidence of fire damage to some of the bones in the Quartzose Sand and Pelletal Phosphorite Members.

Other African localities

African localities other than Langebaanweg which are mentioned in this paper are:

Afar, Ethiopia, comprising mainly the Hadar Formation which appears by radiometric methods to date from 3,1 to less than 2,6 m.y. (Taieb *et al.* 1978; Aronson *et al.* 1977). The Amado Formation is of unknown age. Beglia Formation, Tunisia, aged about 12–13 m.y. (Robinson & Black 1969).

Elandsfontein, near Langebaanweg, a rich site of Middle Pleistocene age with some later fossils (Klein 1978; Hendey 1974: 26).

Fort Ternan, Kenya, dated to 14 m.y. (Gentry 1970*a*; Bishop, Miller & Fitch 1969).

Kaiso Formation, Uganda, thought to span about 5,0–2,5 m.y. and to have an earlier and a later faunal level (Cooke & Coryndon 1970).

Karosit Beds, Kenya, probably a little older than 3,4 m.y. (Bishop *et al.* 1971).

Laetoli, formerly called Laetolil, Tanzania. The Laetolil Beds date from 3,59 to 3,77 m.y., and the later Ndolanya Beds are older than 2,4 m.y. (M. D. Leakey *et al.* 1976; M. D. Leakey & Hay 1979).

Lothagam, Kenya. The Logatham 1 fauna may be about 5,5 m.y. (Behrensmeyer 1976; Smart 1976).

- Lukeino Formation, Kenya, 6,0–6,7 m.y. (Pickford 1975, 1978*b*; Thomas 1979*b*).
- Makapansgat Limeworks, Transvaal, South Africa, where the bovids appear to come between Langebaanweg and Olduvai middle and upper Bed II. The fauna derives from more than one stratigraphic level (Wells & Cooke 1956; Gentry & Gentry 1978: 66; Vrba 1977).
- Mpesida Beds, Kenya, about 7 m.y. (Bishop *et al.* 1971; Thomas 1979*b*).
- Mursi Formation, Omo, Ethiopia, where a basalt overlying the fossiliferous levels has been dated to 4,05 m.y. (Butzer & Thurber 1969).
- Ngorora Formation, Kenya, spanning 12–9 m.y. (Bishop & Pickford 1975; Pickford 1978*a*.)
- Olduvai Gorge, Tanzania, where Beds I to IV span 2,1–0,6 m.y. (M. D. Leakey 1971; Gentry & Gentry 1978).
- Peninj, Tanzania, which correlates faunally and radiometrically with Olduvai middle and upper Bed II (Gentry & Gentry 1978: 292, 62–63).
- Sahabi, Libya, of latest Miocene age, perhaps slightly younger than Wadi Natrun (Maglio 1973: 68, 70; Boaz *et al.* 1979).
- Shungura Formation, Omo, Ethiopia, with an approximate time span from 3,2–0,8 m.y. (Coppens *et al.* 1976; Brown *et al.* 1978). Member B has an age of about 2,8 m.y. and member G an age slightly younger than 2 m.y.
- Sterkfontein Type Site or Main Quarry, Transvaal, South Africa, at which most of the mammalian fauna comes from member 4 with a probable age of about 3,0–2,5 m.y. (Vrba 1976, fig. 20; Partridge 1978).
- Swartklip, southern Cape Province, South Africa, of Upper Pleistocene age (Hendey & Hendey 1968; Klein 1975).
- Wadi Natrun, Egypt, with a poorly known vertebrate fauna, perhaps about 6 m.y. (Andrews 1902; Maglio 1973: 70).

The most frequently mentioned locality outside Africa is the Siwaliks Group in India and Pakistan, which has a sequence of deposits ranging from Miocene to Pleistocene. Pilbeam *et al.* (1977) give a condensed history and much new information on these deposits. At present it appears likely that the bulk of known Lower and Middle Siwaliks faunas fall into two groups. An earlier fauna comes from the upper two-thirds of the Chinji Formation at its type locality and from Ramnagar. It best resembles Astaracian faunas of Europe and west Asia and its age is judged to be about 12–13 m.y. It contains the lophodont pig *Listriodon* but no *Hipparion*. A later fauna comes from the middle part of the Nagri Formation at Nagri, the upper part of the same Formation in the Dhok Mila–Gandakas area and Haritalyangar, and continues through the succeeding Dhok Pathan Formation in its type and adjacent areas. (The Dhok Pathan Formation is known only from its upper levels in the type area.) This later fauna agrees best with Vallesian and Turolian faunas elsewhere and has a likely age range from about 10 to 7,5 m.y. 'Dhok Pathan' fossils collected

in the Hasnot area are somewhat younger, perhaps about 7,0 m.y. *Hipparion* enters the sequence at the poorly fossiliferous base of the Nagri Formation.

Classification

The classification of bovids used here is modified from that of Simpson (1945), with some improvements from Ansell (1971) and some new features:

Family Bovidae

Subfamily Bovinae

Tribe Tragelaphini . Eland, bongo, kudu, mountain nyala, sitatunga, nyala, bushbuck. Mainly browsers in bush and forest.

Tribe Boselaphini . Now represented by only the nilgai and four-horned antelope in India, but formerly occurred in Africa

Tribe Bovini . Cattle and buffaloes, the largest bovids

Subfamily Cephalophinae

Tribe Cephalophini . Duikers, mainly small forest antelopes which are rarely fossilized

Subfamily Hippotraginae

Tribe Reduncini . Waterbuck, lechwes, kob and reedbucks. Grazing antelopes always found in the vicinity of water

Tribe Hippotragini . Roan, sable, oryxes and addax

Subfamily Alcelaphinae

Tribe Alcelaphini . Wildebeests, hartebeests, bastard hartebeests, Hunter's antelope or Tana River hartebeest. Grazing, cursorial antelopes of open country. Includes *Aepyceros*, the impala, usually placed in the Antilopini

Subfamily Antilopinae

Tribe Neotragini . Royal antelope, Bates' dwarf antelope, suni, dik-diks, steenboks, grysbok, klipspringer, oribi, beira. Small antelopes not found in such dense cover as duikers

Tribe Antilopini . Gazelles, springbok, blackbuck, gerenuk and dibatag. Also includes tribe Saigini (containing *Saiga* and *Pantholops* of Asia). Small to medium sized, cursorial antelopes often adapted to conditions of water shortage

Subfamily Caprinae

Tribe 'Rupicapri' . Goral, serow, Rocky Mountain goat. *Rupicapra* itself, the chamois, might be better placed in the Caprini. Not found in Africa

Tribe Ovibovini	.	Musk ox and takin. More abundant earlier in bovid history than they are today
Tribe Caprini	.	Sheep, goats, tahr

The first three subfamilies have been thought to comprise a group called the Boodontia and the second three the Aegodontia (Gentry 1978*b*: 564; Simpson 1945: 270; Pilgrim 1939: 10), but these groups are not used in the formal classification adopted here.

Abbreviations

The present report covers Bovidae which had been incorporated into the collections of the South African Museum by early 1977. All fossils from Langebaanweg are in the South African Museum. Catalogue numbers of these specimens begin with the letters SAM-PQ-L, in which SAM refers to the South African Museum, PQ is a departmental prefix, and L stands for Langebaanweg. Other abbreviations in the text are:

QSM	Quartzose Sand Member of the Varswater Formation
PPM	Pelletal Phosphorite Member of the Varswater Formation
3aS	bed 3aS of the Pelletal Phosphorite Member
3aN	bed 3aN of the Pelletal Phosphorite Member
BM(NH)	British Museum (Natural History), London
BPI	Bernard Price Institute for Palaeontological Research, Johannesburg
KNM	Kenya National Museum, Nairobi
m.y.	millions of years

Specimens from the Omo and Afar in Ethiopia have yet to be lodged permanently in an institution, and only locality and field catalogue numbers are given for them.

Measurements

Measurements are given in millimetres. Tooth measurements were taken on specimens in the earlier or later parts of middle wear. They were not taken on specimens in early or late wear unless this is stated.

Length measurements of limb bones were taken as follows:

Femur—from the lateral end of the articular head to the lowest level of the distal medial condyle

Tibia—from the lowest point of the top medial facet to the projecting tip of bone behind the medial malleolus

Metatarsal—from the highest point behind the medial part of the ecto-cuneiform facet to the medial side of the most projecting part of the distal medial condyle

Humerus—from the top of the lateral tuberosity to the lowest point of the medial side distally

Radius—from the centre of the medial edge of the proximal medial facet

to the lowest point of the ridge on the scaphoid facet medially Metacarpal—from the edge of the proximal articular facet above the insertion for the extensor carpi radialis to the median side of the most projecting part of the distal medial condyle

Terms

Five terms used frequently in the text need explanation:

The *basal index* of a horn-core is a pair of measurements given in the form $46,9 \times 37,2$ in which the first is the anteroposterior diameter at the base and the second the mediolateral diameter at 90° to the first

Horn-cores are said to be *obliquely inserted* when their inclinations are low in side view. It is the opposite condition from upright insertions

Horn-cores with any degree of curvature frequently have *torsion*. This may be clockwise or anti-clockwise and is described as it exists in the right horn-core

A *basal pillar*, when it occurs, is found in the centre of the medial side of upper molars or the lateral side of lower molars, completely or partly separate from the rest of the occlusal surface. In the Cope-Osborn nomenclature it is the entostyle of an upper and ectostylid of a lower molar

A *goat fold* is a transverse flange at the front of the lower molars.

BOVIDAE FROM 'E' QUARRY

Tribe Tragelaphini

Tragelaphus spp indet.

Figs 1–4.

Material

A number of tragelaphine horn-cores from 'E' Quarry at Langebaanweg belong to a species about the size of the living nyala, *Tragelaphus angasi*. They are:

L5252—basal half of a right horn-core

L5868—base of a left horn-core

L5922—base of a right, index $42,1 \times 41,4$

L5924—base of a right, index $39,1 \times 38,8$

L6568—basal half of a right, index $40,1 \times 42,3$ (Fig. 1)

L6574—basal half of a left

L40056—base of a right, index $39,2 \times 41,6$

L4620, L5255, L6079, L6081, L6083, L6084, L6379, L6571, L6576, L41039
—parts of left horn-cores

L5253, L5716B, L5920, L6435, L6569, L6570, L6575, L6583, L6584, L13983
—parts of right horn-cores

In addition, there is an occipital surface, L5085, of appropriate size to be conspecific with the horn-cores. The height of the occipital, measured from the dorsal edge of the foramen magnum, is $41,3$.



Fig. 1. *Tragelaphus* sp. L6568, anterior view of right horn-core.
Scale = 50 mm.

L40056 and L41039 of the above listed material are definitely from bed 3aS of the PPM. The rest is probably also from 3aS but a few may be from the QSM.

Parts of left and right horn-cores, L13164 and L22556 additional to the above list, do come from the QSM.

Parts of two left and right horn-cores, L33779 and L33833, come from bed 3aN of the PPM. Also probably from 3aN is L40759 (Fig. 2), the greater part of a left horn-core with a rather damaged base and an index of $42,2 \times 46,3$.

Horizon

Tragelaphus is much better represented in bed 3aS than in either 3aN or the QSM. Nearly all the horn-cores were picked up by mine workers, many in 1966-7, and were not recovered from controlled excavations.

Description

On horn-core L6574 the posterolateral keel is weaker than the anterior one and can hardly be seen at all. This may have been an unusual individual in life or the fossil may have suffered water rolling after death. In the other horn-cores the posterolateral keel is always strong. The anterior keel is rarely as strong as the posterolateral one, but it can be seen to be so at the very bases of L5252, L5868 and L6568. A part of a left horn-core, L33779, is about 140 mm long and has a strong groove alongside, or instead of, a keel. In comparison with the living, similarly sized species *Tragelaphus angasi* and *T. spekei*, the horn-cores are less compressed anteroposteriorly, inserted more uprightly, and look as if they were inserted less far behind the orbits. The insertions must

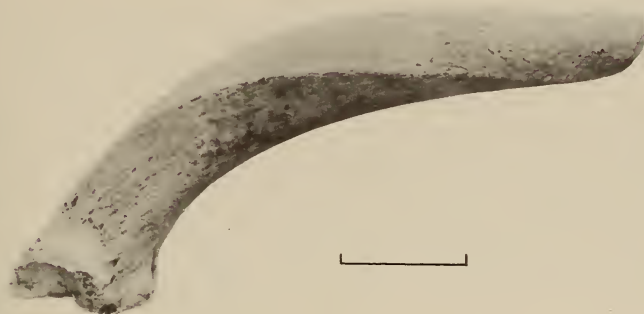


Fig. 2. *Tragelaphus* sp. L40759, lateral view of left horn-core.
Scale = 50 mm.

have been wider apart than at the present day, and this could be linked with the anteroposterior level of the insertions above the back of the orbits rather than just behind them. L6568 and L44056 certainly show a greater width of frontals on the medial side of the horn bases than can be seen in living *Tragelaphus*. The degree of basal divergence can be seen in anterodorsal view on the horn-cores L5922, L6568 and L40056, and it was greater than in *T. angasi* and *T. spekei* or any other tragelaphine alive today. The degree of spiralling in the Langebaanweg horn-cores is about as strong as in *T. angasi* and *spekei*. There are no sinuses within the horn pedicels. Most of the characters whereby this species differs from equivalent sized living species can be paralleled in the smaller horn-cores of an extinct bushbuck, L144-1 and 2 from member C of the Shungura Formation. (However the width apart of the insertions and the basal divergence are not known in the Omo fossils.) Such characters appear to be primitive in the small and medium sized lineages of *Tragelaphus*.

Two of the three horn-cores from bed 3aN deserve particular mention. L40759, probably from 3aN, is larger than the main mass of 3aS horn-cores (Fig. 3) and has a preserved length of about 280 mm. It is strongly spiralled, in fact, almost as much as in the living greater kudu, *Tragelaphus strepsiceros*. Its anterior keel is stronger basally than the posterolateral one, unlike other 'E' Quarry *Tragelaphus*, but by the tip of the preserved part of the horn-core the posterolateral keel has become strong and sharp. Through being more spiralled, the line of the posterolateral keel near the base is more strongly concave than in the other horn-cores. Finds from the Shungura and Mursi Formations (Gentry 1976: 276-7, 288; a fuller account is awaiting publication) suggest that *T. strepsiceros* evolved from ancestors of smaller size and with horn-cores showing a stronger posterolateral keel and a weaker anterior keel, no medio-lateral compression, weaker spiralling and less upright insertions. One could anticipate difficulties in distinguishing members of this lineage from relatives or ancestors of *T. spekei* at sites coeval with, or earlier than, the Mursi Formation. Possible kudu horn-cores from the Mursi Formation, particularly the base

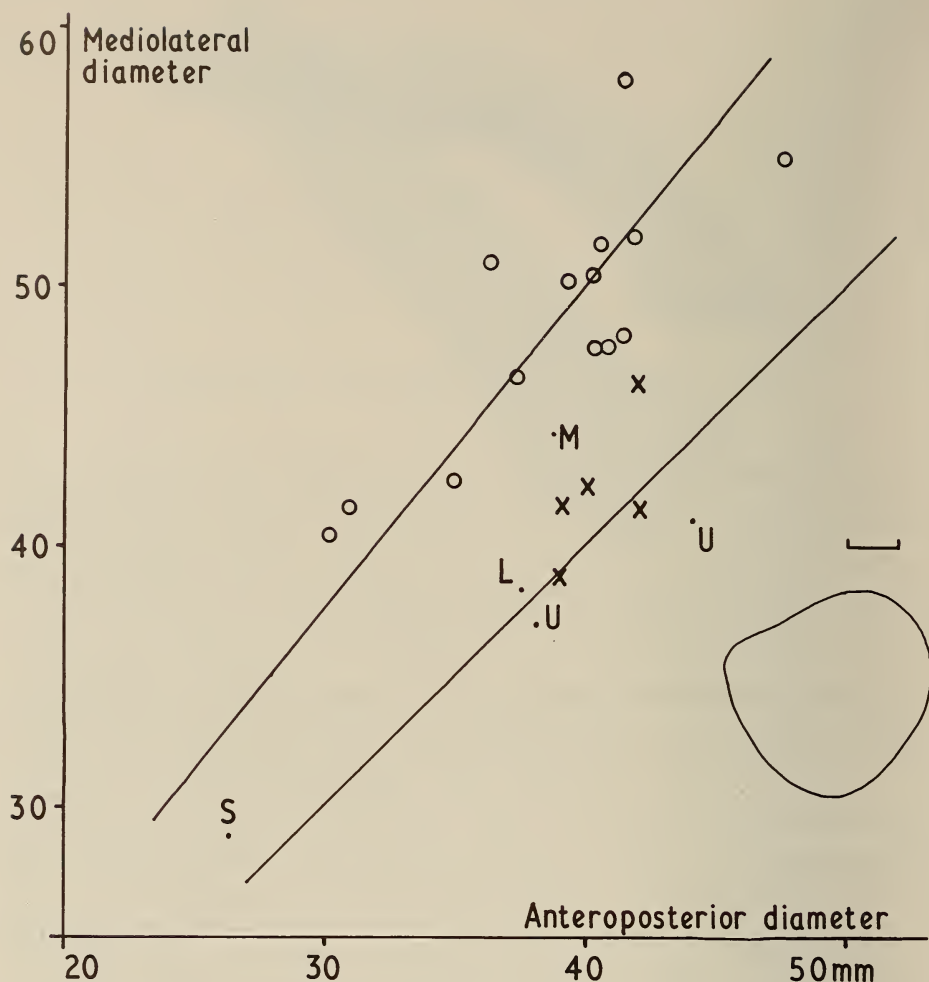


Fig. 3. Basal dimensions of *Tragelaphus* horn-cores. X = E Quarry Langebaanweg, O = extant *T. spekei*, M = Mursi Formation YS 68.2078, L = Makapansgat Limeworks BPI M 490, S = *T. ?pricei* from Shungura Formation, U = Lukeino Formation (from Thomas 1979b). The highest X is L40759. The lower diagonal line is that along which mediolateral diameter is 100 per cent of anteroposterior diameter; the upper line is 125 per cent. A cross-section of the right horn-core L6568 is shown, taken 20 mm above its base, with lateral side to the left and anterior side to the base. Scale = 10 mm.

of a right horn-core YS 1968-2078 with a basal index $38,7 \times 44,3$ (Fig. 3), are about the same size as L40759, have a posterolateral keel stronger than the anterior one, weaker spiralling than L40759, and about the same inclination and degree of compression. Thus, if L40759 were a different species from other Langebaanweg horn-cores and on the kudu lineage, it would be at about the level of member E or F of the Shungura Formation by its keels and even later

by its strong spiralling. If it is a different species from the other 'E' Quarry horn-cores, it is probably a precocious southern Cape development unrelated to the *T. strepsiceros* lineage.

L33833, the fragment of a large right horn-core from bed 3aN, has an index of $48,5 \times 49,5$ at its lowest level which is not known to be the original base. This is larger than other tragelaphine horn-cores likely to be from 3aS. It appears to have little spiralization, but its large size makes the comparison difficult. The posterolateral keel is the most prominent as in most Langebaanweg horn-cores, and the anterior keel is also well developed. Either or both L40759 and L33833 could represent additional species of tragelaphines in the Langebaanweg fauna.

The occipital surface L5085 shows its tragelaphine affinities in its rather flat surface, a median vertical ridge without flanking hollows, traces of a small, narrow mastoid and a horizontal top edge centrally.

One of the interesting features of the Langebaanweg assemblage is the problem of finding teeth which might be conspecific with the tragelaphine horn-cores. This question will be taken up later and all that need be stated here is that only a few teeth such as the right M_3 L4628 (Fig. 4) are candidates for being tragelaphine. This tooth probably comes from the PPM, is in middle wear, and has an occlusal length of 29,2. It resembles M_3 s of *Mesembriportax acrae* except in being rather small. A moderately developed metastylid is present, there is a tiny basal pillar, and the medial wall of the back lobe of the tooth is set obliquely. The wear is abnormal in that the occlusal surface slopes steeply down towards the buccal edge.

Comparisons

The base of a tragelaphine right horn-core, BPI M490 with basal index $37,6 \times 38,3$, and possibly another fragment, M491, from Makapansgat Lime-works are about the size of the Langebaanweg species, and agree with it in having the anterior keel no better developed than the posterolateral one and in being less compressed anteroposteriorly than in living *T. angasi* and *T. spekei*. Dentitions of appropriate size to go with the horn-cores have already been assigned to *T. cf. angasi* by Wells & Cooke (1956: 10).

A right horn-core of a *Tragelaphus*, BM(NH) M 26402, from the early assemblage of the Kaiso Formation (Cooke & Coryndon 1970: 200; Gentry & Gentry 1978: 305) is about the same size as the Langebaanweg species but more anteroposteriorly compressed, having a basal index of $41,0 \times 50,0$. The early Kaiso assemblage has been thought to have an age of about 5 m.y. (Cooke & Coryndon 1970: 220, fig. 17; Maglio 1973: 70), but Gentry & Gentry (1978: 64) thought that the bovids could as easily fit a later age.

Thomas (1979b, fig. 2) has recorded a fine frontlet and two partial horn-cores of *Tragelaphus cf. spekei* from Lukeino which are very like the Langebaanweg horn-cores, but slightly less compressed anteroposteriorly. He gives basal indices of 38×37 and 44×41 . Tragelaphine teeth are also present at Lukeino



Fig. 4. *Tragelaphus* sp. L4628, occlusal and lateral views of right M_3 . Scale = 10 mm.

and Mpesida (Thomas 1979b, pl. 2 (figs 4, 8–9, 11, 14)). Gentry (1978a: 297) pointed to the appearance of tragelaphine-like teeth as early as Ngorora.

Tribe Boselaphini
Genus *Mesembriportax*

Type species

Mesembriportax acrae Gentry, 1974.

Mesembriportax acrae Gentry, 1974
Figs 5–6

Remarks

Since Gentry (1974) described *Mesembriportax acrae* from Bed 2 (= QSM) of 'E' Quarry, Langebaanweg, a number of new specimens have come to light from both the QSM and PPM. The two chief ones (Figs 5–6) are:

L25870—cranium with both horn-cores attached, other fragmentary skull



Fig. 5. *Mesembriportax acrae*. L40071, dorsal view of cranium; L25870, lateral view of cranium
Scales = 50 mm.

bones, the maxillary tooth rows, both mandibles, and parts of cervical vertebrae. It comes from the QSM

L40071—cranium with right horn-core attached, much of the left horn-core, and fragmentary skull bones. This comes from bed 3aS.

Other remains include the partial frontlets and skull fragments L20918 and L22005, both from the QSM. The latter has some upper teeth as well as quite a lot of other dental remains.

In both L25870 and L40071 the frontals are preserved further forward than in the holotype L13101. Thus it can easily be seen that their horn-core insertions



Fig. 6. *Mesembriportax acrae*. L25870, occipital and ventral views of cranium.
Scales = 25 mm.

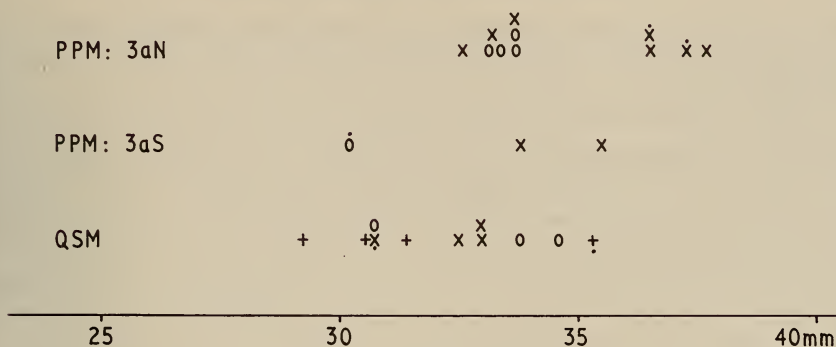


Fig. 7. Occlusal length of M_3 in *Mesembriportax acrae*. X = right side, O = left side, + = both sides. Dotted readings are in later wear.

are slightly closer than on the holotype (Gentry 1974, fig. 2). Moreover, the divergence of the horn-cores is much less, the torsion is less strong, and the dorsal parts of the orbital rims project more strongly. These characters bring L25870 and L40071 closer to *Miotragocerus*, especially *M. amalthea*, a fairly large and advanced species from Pikermi, Greece, and other sites of Turolian age.

Other characters show the variation among the Langebaanweg specimens but do not correlate with the geology of the site. Compared with L13101, L25870, likewise from the QSM, shows a stronger approach to a posteromedial keel, more oblique horn-core insertions, a more sharply localized raising of the frontals between the horn-core bases, almost certainly a less sloping braincase roof, and a braincase which does not widen posteriorly. However, L40071, which is more like the QSM holotype for these characters, itself comes from the PPM. Besides L40071, there are other, less well preserved, remains of *Mesembriportax acrae* from the PPM. No valid differences between them and the remains from the QSM were found, but it appears from a comparison of M_3 occlusal lengths that there could have been a size increase (Fig. 7). This is also shown by a statistical comparison of both M_2 and M_3 occlusal lengths:

		Number measured	Mean	Range	Standard deviation	Standard error
M_2	QSM	12	23,7	20,8–25,9	1,5	0,42
	PPM:3aS	3	24,5	23,9–25,3	0,7	0,42
	PPM:3aN	3	24,7	23,8–25,7	1,0	0,55
M_3	QSM	9	32,3	29,2–35,3	2,0	0,66
	PPM:3aS	2	32,0	30,2–33,8	—	—
	PPM:3aN	6	35,2	32,6–37,7	2,3	0,92

The values of T for M_2 s and M_3 s in the QSM and bed 3aN were 1,14 and

2,65, the latter alone being significant at the 5 per cent level. The measurements were confined to teeth in middle wear, and each sample was from either the left or right side alone.

Gentry (1974: 180) compared the dental characters of *Mesembriportax acrae* and *Miotragocerus* and stated that the former had straighter medial walls of its lower molars. In addition, the P_4 of the *Mesembriportax acrae* holotype had a more massive metaconid with less differentiation into a neck and strong anterior and posterior flanges, the paraconid had the form of a low protuberance from the parastylid rather than a flange, and the hypoconid projected more strongly than in many *Miotragocerus*. In the P_4 of L20508 only the last difference appeared valid. This statement can be modified now that more is known of variation during wear in *Mesembriportax acrae*. Of a dozen mandibles of *M. acrae* with P_4 , six were held to be in early or early middle wear and the remainder in late middle or late wear. Five P_4 s out of the six in earlier wear had flanges anteriorly and/or posteriorly on the metaconid, while four of the six in later wear had scarcely any traces of flanges. Again, four of the first group had the paraconid of P_4 in the form of a flange and five of the second group had it merely as a low protuberance from the parastylid. Seven out of the whole twelve had a fairly projecting hypoconid on P_4 and four had a fusion between paraconid and metaconid (the latter character not mentioned by Gentry 1974), but these characters were uncorrelated with wear. A similar loss of definition of the various flanges can be seen during wear in *Miotragocerus amalthea* from Pikermi, but it does seem that the paraconid flange is more marked in this species. In the author's revised opinion this becomes one of two good differences in the P_4 s of the two species. The other is that paraconid-metaconid fusion is far more infrequent in *M. amalthea*; it occurred in only one out of twenty-six examples from Pikermi. The straighter medial walls of the lower molars in *Mesembriportax acrae* appear to be present in only about a third of the specimens—seven out of twenty-four.

Revised diagnosis

The diagnosis of *Mesembriportax acrae* (Gentry 1974: 148) should therefore be modified and reduced to the following. A moderate to large boselaphine with short to fairly long horn-cores. Horn-cores with varying insertion angle, basal divergence and width apart of insertion positions. Horn-cores compressed mediolaterally and with a posterolateral keel and a strong slightly helical anterior keel in their lower part, the anterior keel being stepped at its top and the succeeding distal part of the horn-core being of small circular cross-section. In so far as any torsion exists, its direction is anti-clockwise in the right horn-core. Divergence of the horn-cores lessens distally, and there is little or no backward curvature. Frontals extensively hollowed internally, and their top surface raised much above the level of the top of the orbits; braincase in line with or slightly angled on the face axis; top of braincase not curved downward posteriorly above the occipital surface; strong temporal ridges on braincase

roof not approaching closely posteriorly and with a rugose surface between them; orbits sometimes without a projecting dorsal rim; small supraorbital pits; nasals long and narrow with large central flanges anteriorly but no lateral flanges; large preorbital fossa; infraorbital foramen low and situated above the posterior margin of P^2 ; premaxillae narrow anteriorly but with strong ascending rami of approximately even width throughout and with a wide contact on the nasals; palate very wide; median indentation at the back of the palate well behind the level of the lateral indentations; occipital surface with a squared outline; large mastoid exposure of periotic; anterior tuberosities of basioccipital fairly wide apart and not very large.

Brachyodont or only moderately hypsodont cheek teeth, with not very rugose enamel; small basal pillars on upper and lower molars; medial lobes of upper molars not joined to one another or to the lateral side of the tooth until late in life; mesostyles quite strong on upper molars; central cavities of upper molars not very complicated in outline; medial walls of lower molars sometimes rather flat; lower molars sometimes with a small goat fold (a transverse flange at the front of the tooth); M_3 often with a large central cavity in the rear lobe during early wear and often with a rear flange; long premolar rows with large anterior premolars; paraconid and metaconid more often unfused than fused on P_4 ; paraconid of P_4 has the shape of a low protuberance or small flange on the back of the parastylid; hypoconid sometimes projecting on P_4 ; I_1 s not greatly enlarged.

Measurements

Measurements on the two most complete new crania of *M. acrae* are:

	L25870	L40071
Length of horn-core along anterior keel . . .	310	420
Anteroposterior diameter at base of horn-core .	66,3	72,2
Lateromedial diameter at base of horn-core .	47,2	51,2
Minimum width across lateral sides of horn pedicels	140,0	—
Occipital height from dorsal edge of foramen magnum	49,5	51,9
Skull width across mastoids behind external auditory meatus	121,4	124,6
Width across anterior tuberosities of basioccipital	28,2	28,0
Width across posterior tuberosities of basioccipital	46,0	40,6
Occlusal length M^1-M^3	67,9	—
Occlusal length M^2	24,3	—
Occlusal length P^4	14,7	—

Measurements on new more fragmentary skull remains are:

	L22005 QSM	L22051 QSM	L22056 QSM	L30211 3aN	L32401 3aN	L41689 QSM/3aS
Length of horn-core along anterior keel . . .	—	—	—	—	—	330
Anteroposterior diameter at base of horn-core .	60,1	—	—	69,5	—	79,8
Lateromedial diameter at base of horn-core .	43,6	—	—	41,6	—	38,5
Width across anterior tuberosities of basi-occipital	29,1	27,6	24,6	—	28,0	—
Width across posterior tuberosities of same	37,7	36,1	39,6	—	42,9	—

Some measurements on the more complete dentitions in middle wear are shown in Table 1. All are likely to be from different individuals.

TABLE 1
Measurements of boselaphine dentitions.

	L20985 QSM	L25870 QSM	L28327 QSM	L46059 3aN	L20542 QSM	L21744 QSM
Occlusal length M_1-M_3	69,0	70,8	76,8	81,6	—	—
Occlusal length M_2	21,6	23,0	25,0	25,7	—	—
Occlusal length M_3	29,2	30,6	30,7	33,7	—	—
Occlusal length P_2-P_4	48,7	51,0	c. 53,7	53,2	*51,5	*52,7
Occlusal length P_2	14,3	15,7	16,2	15,5	*11,0	*12,9
Occlusal length P_4	17,4	17,7	—	20,3	*25,3	*25,1
Ramus depth below P_2	34,8	36,9	—	31,9	—	—
Ramus depth below M_1	39,7	39,3	37,8	—	—	—
Ramus depth below M_3	44,0	41,1	39,2	—	—	—
	L25033 QSM	L25870 QSM	L32401 3aN			
Occlusal length M^1-M^3	70,1	67,9	68,4			
Occlusal length M^2	25,3	24,3	23,7			
Occlusal length P^2-P^4	—	—	55,7			
Occlusal length P^4	15,3	14,7	15,5			

* = deciduous dentition

Occlusal lengths of other teeth in middle wear are as follows:

L14253 left P^4 15,7 QSM; L20982 right P^4 15,4 QSM; L22253 right P^4 15,2 QSM; L41720 left P^4 17,9 PPM

L21828 left dP^3 20,9, dP^4 20,2 QSM

L11350 left P_4 21,9; L22369 left P_4 20,6 QSM; L32792 right P_4 18,0 PPM; L40976A right P_4 19,4 PPM; L41689 left P_4 15,4 PPM; L41720 right P_4 21,4 PPM.

L24651 left dP_4 25,3 QSM; L30948 left dP_4 29,9 PPM; L31076 right dP_4 27,5 PPM

Comparisons

Because of the resemblances of the new material to *Miotragocerus* it is necessary to revise the account of differences between *Mesembriportax acrae* and other boselaphines from that given in Gentry (1974: 179–181). The most important comparison lies with *Miotragocerus amalthea*, a species which has considerable variation of its horn-cores (Pilgrim & Hopwood 1928: 46–49). The Langebaanweg species is now seen to have differences in its larger size, less mediolateral compression of the horn-cores, even less backward curvature of its horn-cores, a longer terminal portion of its horn-cores distal to the top of the anterior keel, horn-cores usually more divergent, frontals raised to a higher level between the horn-core bases relative to the dorsal part of the orbital rims and hence with a more extensive system of internal sinuses, perhaps a better rugose surface on the braincase roof behind the horn-cores, and a squarer outline of the occipital surface. For most of the differences the South African species can be plausibly supposed to be more advanced.

Another *Miotragocerus* species at Samos is larger than *M. amalthea*, and includes material named *M. curvicornis* and *M. recticornis* (Andree 1926). This species is unlike both *M. amalthea* and the Langebaanweg species in that its horn-cores have little or no demarcation of a distal portion with a rounded cross-section.

The remaining principal species of *Miotragocerus* were listed by Gentry (1974: 175). Among these *M. gradiens* is a small, primitive species and *M. pannoniae* and *M. leskewitschi* are later but still small species. *M. spectabilis* is a larger and later species from China similar to *M. amalthea*. *M. valenciennesi* is a small to moderate sized species coexisting with *M. amalthea* at Pikermi, and *M. browni* is a moderate sized Siwaliks species, perhaps descended from the earlier *M. gradiens*.

The only fossils of *Miotragocerus* from Africa are the record from Lothagam (Smart 1976: 365) and a frontlet with much of its horn-cores from Sahabi, now in Rome. The latter was taken by Thomas (1979a: 268, pl. 1 (figs 5a–5b)) as holotype of a new species *M. cyrenaicus*. It differs from the Langebaanweg species by being probably somewhat smaller and its horn-cores more strongly compressed mediolaterally, slightly curved backward, and with no sharp diminution of anteroposterior diameter distally. This last character causes it to resemble the Samos examples of *M. curvicornis* and *M. recticornis* rather than *M. amalthea*. Its horn-cores are strongly divergent and with little sign of a posteromedial keel as in the *Mesembriportax acrae* holotype, but their insertion angle is lower and they have less torsion. It also differs from the holotype by having projecting rims to its orbits dorsally. It is not likely to belong to the caprine *Pachytragus* which occurs in the earlier pre-*Hipparion* and *Hipparion* levels of the Beglia Formation (Robinson & Black 1969; Robinson 1972) because of the wider insertion of its horn-cores, and the anterior keel extending low on the pedicel to below the level of the lateral and medial sides. The low inclination and wide divergence of the horn-cores are also unlike *Pachytragus*.

Mesembriportax acrae differs from *Miotragocerus browni* by its greater size, wider skull and the horn-cores being shorter, not curved backward and with the anterior keel terminating well below the horn-core tip.

The characters distinguishing *Mesembriportax acrae* from *Protragocerus* as a whole are fewer than given by Gentry (1974: 179). They now comprise greater size, sinuses in the frontals, braincase roof not curved downward posteriorly, presence of a rugose surface between the temporal ridges, and a larger basi-occipital with stronger anterior tuberosities. These differences continue to be more impressive than those separating *M. acrae* from *Miotragocerus*.

It seems that in Europe *Miotragocerus* does not usually occur as early as *Protragocerus*. It is known back to the Vallesian and has one late Astaracian record (*M. monacensis* Stromer, 1928, of 'Sarmatian' age, the type species of *Miotragocerus*). Thus, according to the biozones set up by Mein (1975), it occurs from zones 12 or 13 back to 9 or perhaps 8. *Protragocerus*, as recorded from such sites as Belomechetskaya, Despotovac, Atzgersdorf, Hollabrunn, Sommerein, and La Grive St Alban (Thenius 1956, 1959), is of Astaracian (= late Vindobonian and 'Sarmatian') age, equal to Mein's zones 6 to 8. In the Siwaliks *Miotragocerus gradiens* occurs together with *Protragocerus* in the Chinji fauna, thought to be of Astaracian-equivalent age, but *Miotragocerus* also survives until the Dhok Pathan Formation (Pilbeam *et al.* 1977). Thus, *Miotragocerus* is generally younger than 12 m.y. whereas *Protragocerus* is from 12 to 14 m.y. Relationships of these early boselaphines are poorly understood, but it seems that *Protragocerus* could well be a stem genus from which *Miotragocerus* and other genera took their origins—cf. Gentry (1974, fig. 27) in which *Miotragocerus* is shown having an ancestry independent of *Protragocerus*.

If *Mesembriportax acrae* were to be described as a new species in this paper, one might well decide to put it into *Miotragocerus* as, indeed, Thomas (1979a: 273) has suggested. However, for the present *Mesembriportax* will be retained. *M. acrae* is not very like the north African *Miotragocerus cyrenaicus* and it is still possible that it is an independent line of descent from an African *Protragocerus*.

Tribe Bovini

Simatherium Dietrich, 1941

Simatherium Dietrich, 1941: 221.

Simatherium Dietrich, 1942: 119.

Type species

Simatherium kohllarseni Dietrich, 1942: pl. 20 (figs 161, 163, 165).

Generic diagnosis

Extinct moderate to large sized African Bovini with short to moderately long horn-cores, rather massive for the size of the skull. Horn-cores slightly compressed mediolaterally or without compression, sometimes with an anterior keel, of irregular or rounded rather than neatly triangular cross-section, inserted

just behind the orbits, inserted widely apart, with moderate to strong divergence, gently curved backward in side view, and without torsion. Horn-cores sometimes with deep longitudinal grooves.

Frontals and horn pedicels with quite extensive, irregularly shaped internal sinuses, braincase short, braincase roof sloping a little downward posteriorly, temporal ridges present, a rugose raised area at the back of the braincase roof where temporal ridges converge toward the top of the occipital surface, occipital broad and low, with horizontal top edge and with some development of hollows dorsally on either side of the median vertical ridge. Nuchal crests strong. Moderate to large mastoid. Basioccipital wide posteriorly and triangular, with a short central longitudinal valley between the posterior tuberosities, with a central longitudinal ridge in the area just behind the anterior tuberosities, with small localized anterior tuberosities and poor or no longitudinal ridges behind them.

Remarks

The single species hitherto known of *Simatherium* is represented by a poorly preserved cranium from the Vogel River, Laetoli, kept in the Palaeontological Museum of Humboldt University, East Berlin, no. Vo 670. Its precise stratigraphical provenance is unknown but Dietrich (1942; 1950: 49) assigned it to the oldest of the faunas from this area. Some isolated bovine teeth (Dietrich 1950, pl. 1 (fig. 5), pl. 3 (figs 32, 36)) are probably of *S. kohllarseni*. By invitation of M. D. Leakey, the writer has been able to see a bovine cranium recently recovered from the Laetolil Beds (as defined by M. D. Leakey *et al.* 1976), which appears to be a second specimen of *S. kohllarseni*. *Simatherium* is a possible ancestor for *Pelorovis*, the extinct long horned 'buffaloes' of the African Pleistocene (Gentry & Gentry 1978: 311). It is more primitive than *Pelorovis*, and, therefore, has some similarity to *Ugandax*, a genus probably ancestral to the extant *Syncerus*.

The choice for generic identity of the Langebaanweg bovine lay between *Ugandax* and *Simatherium* and finally the latter was chosen, although with mainly primitive forms the balance of evidence is not overwhelming.

Simatherium demissum sp. nov.

Figs 8-13

Holotype

L45001—nearly complete left and right cores with midfrontals suture, left mandible with P_2 - M_3 , left M^2 , right P^2 , parts of occipital surface, basioccipital, all found associated (Figs 8-11).

Referred material

The main specimens assigned to this species are as follows.

From QSM:

L20905—left M_3 , occlusal length c. 37.4, early middle wear

L21297—right dP^3 , dP^4 , M^1 - M^3 , left dP^3+dP^4 ; unworn right P^2+P^3 and left P^2 - P^4

L25861—right and left mandibles with P_2 - M_3 , upper dentitions, early middle wear. Skull fragments and postcranial parts (Fig. 10)

L28328—left mandible with M_2 + M_3 , early middle and distorted wear

Probably from QSM:

L23400—crushed cranium with horn-cores. Isolated teeth of upper dentitions in late middle wear. Fragments of skull, vertebrae and postcranial bones

From bed 3aS:

L40094—right mandible fragment with M_3 , occlusal length 39,3, late middle wear

L41709—left mandible with P_3 - M_3 , middle wear

L41736—left mandible with P_3 - M_3 , early middle wear

Probably from 3aS:

L11981—right M^3 , occlusal length 35,1, late middle wear

L12116—left mandible fragment with damaged M_3 , occlusal length *c.* 43,0, early middle wear

Probably from bed 3aS, but a few possibly from QSM:

L4615—fragment of right horn-core, index = $82,9 \times c. 77,0$. Piece of horn-core about 160 mm long

L6586—fragment of left horn-core

L1843—left maxilla with dP^2 - dP^4 , right mandible with dP_2 - M_1

L2051—right M_3 , occlusal length 39,5, late middle wear

L4774—right M^3 , occlusal length 37,2, late middle wear

L6599—left mandible fragment with P_3 + P_4 , occlusal length P_4 25,3, in late middle wear

L7255—left P^4 , occlusal length 18,7, early middle wear

From bed 3aN:

L30174—complete but weathered right horn-core, left horn-core incomplete at base, basioccipital, back of braincase

L30175—frontlet with complete horn-cores, skull fragments, basioccipital and part of sides of braincase, right and left maxillae each with P^4 - M^3 in late middle wear (Fig. 9)

L30880—fragment of left horn-core

L30888, L30889—bases of horn-cores

L32609—left and right mandibles with P_2 - M_3 , middle wear

L33380—right mandible with dP_2 - M_1 , occlusal lengths dP_2 - dP_4 65,2, dP_4 30,7

L33841—right mandible with P_2 - M_3 , late middle wear

L45029—right mandible with P_2 , occlusal length 16,2, ramus depth below P_2 37,9

L46058—right mandible with M_1 - M_3 , early wear

L46073—left mandible with P_4 - M_3 , early middle wear

Locality

The holotype is from bed 3aN of the PPM. The provenance of other speci-



Fig. 8. *Simatherium demissum*. L45001, holotype. Dorsal view of left horn-core and frontal; dorsal and occipital views of cranium. Scale = 25 mm.



Fig. 9. *Simatherium demissum*. L30175, anterodorsal view of frontlet with cross-section of right horn-core at level shown. Lateral side of cross-section to the left and anterior side to the base. Scale = 50 mm for frontlet and 25 mm for cross-section. L45001, holotype. Lateral view of right horn-core. Scale = 50 mm.

mens has already been given, and it can be seen that *Simatherium demissum* is represented in the QSM and both beds of the PPM.

Diagnosis

Horn-cores with a strong anterior keel, without much tendency to a postero-lateral keel, with some rounding of the cross-section on either side of the anterior keel so that its shape, even near the base, is not neatly triangular, horn-cores inserted at a low inclination in side view, strongly divergent basally in anterodorsal view and curving strongly so that at the tips they are parallel or even slightly convergent. Slight backward curvature of the horn-cores is not confined to their basal sector. Sometimes with deep longitudinal grooves on posterior surfaces of horn-cores. Localized rugose areas on the front of the pedicels below and in line with the anterior keels.

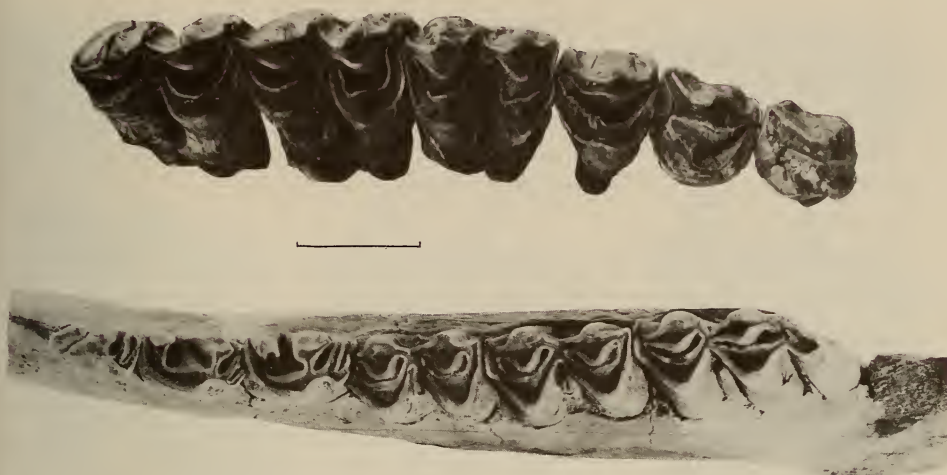


Fig. 10. *Simatherium demissum*. L25861, occlusal view of right upper cheek tooth-row. L45001, holotype, occlusal view of left lower cheek tooth-row. Scale = 25 mm.

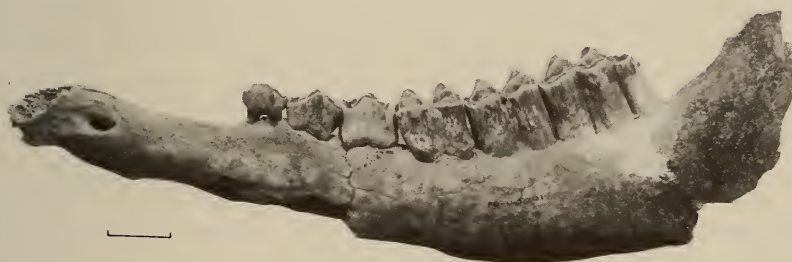


Fig. 11. *Simatherium demissum*. L45001, holotype. Lateral view of left mandible. Scale = 25 mm.

Internal sinuses of frontals and horn pedicels reaching as much as 15 mm above the top of the pedicels, small supraorbital pits, frontals not raised between horn-core bases and no higher than dorsal part of orbital rims, dorsal part of orbital rims projecting quite strongly. The parietofrontals suture has a shallow V-shaped outline pointing forward. Temporal ridges well marked. Median vertical occipital ridge with some development of flanking hollows at the top. Mastoid moderate sized. Basioccipital long, narrowing fairly abruptly just in front of the posterior tuberosities.

Cheek teeth large and only moderately hypsodont with rugose enamel, basal pillars present and of moderate size but simple outline, diminishing in size from front to back of the upper and lower tooth-rows, central cavities with fairly simple outline, styles moderately strong on upper molars, ribs quite large but not very localized on lateral walls between styles, transverse goat folds

practically absent at front of lower molars but mesostylid well developed, out-bowings on front and back of parts of medial walls of lower molars quite well localized as ribs, back lobe of M_3 often with a posterior flange and with only a small or no central cavity, P_4 with hypoconid not projecting very far, metaconid slanted diagonally backward but sometimes with an incipient forwardly directed flange, paraconid quite distinct from parastylid.

Etymology

The name is from the Latin *demissus*, drooping, and refers to the low inclination of the horn-cores.

Remarks

Most of the fossils of *Simatherium demissum* are fairly broken up, but the parts which have survived are well preserved, and the total assemblage allows one to acquire a good idea of much of the cranial morphology. The two horn-core pieces L4615 and L6586 were previously misidentified as from a kudu of similar size to the Olduvai Bed II *Tragelaphus strepsiceros grandis* (Gentry in Hendey 1970: 114). Two characters in this species are primitive among bovines: the rather low-crowned cheek teeth and the closeness of the horn-core insertions to the back of the orbits, indicating that the insertions have not started their evolutionary migration backward on the skull. Other characters which can reasonably be taken as primitive are the backward curvature of the horn-cores in profile, temporal ridges approaching relatively closely posteriorly on the braincase roof, relatively high rather than low and wide occipital surface, and rather smooth anterior tuberosities of the basioccipital.

Isolated teeth of *Simatherium demissum* are not always easily told from the teeth of *Mesembriportax acrae* especially those of larger size from bed 3aN. One may hope that bovine teeth will show all or many of the following characters: larger size, more hypsodonty, larger basal pillars, more rugose enamel, ribs stronger in relation to the mesostyles on the upper molars, less flattened medial walls on the lower molars, stronger mesostylids (contrasting with less of a tendency to goat folds on the lower molars), central cavity absent or small and more restricted to the anterior part on the third (rear) lobe of M_3 (Fig. 12).

A number of limb bones are likely by their size and morphology to belong to the Bovini. Two associated sets are, firstly, distal left humerus L12764, distal left radius L12762 and complete left metacarpal L12763 from the QSM, and, secondly, distal left humerus and complete left metacarpal from the QSM or bed 3aS, both numbered L41704 (Fig. 13). The two metacarpals have lengths and least transverse thicknesses of $268 \times 32,0$ and $253 \times 34,8$ respectively, and are less short and thick than in Pleistocene and Recent Bovini (Fig. 14). A right calcaneum and left astragalus, L40773 from bed 3aS, are also associated with one another. Other bovine limb bones are:

L9992—proximal right radius probably from PPM

L21306—proximal right radius from QSM (Fig. 13)



Fig. 12. Occlusal and lateral views of left M_3 s. From the left: *Mesembriportax acrae* L46592; Bovini, presumably *Simatherium demissum* L50612, L50663. Scales in millimetres.

L6094, L9740—distal right radii probably from PPM

L20445—complete right metacarpal, probably from QSM, with length and least transverse thickness of 225×35.0 .

L12279—left proximal metacarpal probably from PPM

The distal humeri have slanted condyles, a fairly deep hollowing for the lateral humeroradial ligament, a wide distal end of the lateral surface behind the ridge demarcating the hollow for the humeroradial ligament, and a coronoid fossa which is moderately deep. Both proximal radii show a moderately large lateral tubercle which is set low, a rim on the medial side of the medial facet, and a lateral facet which sticks well forward anteriorly. L9992 has an angled edge to its medial facet, whereas L21306 is rounded, and L9992 is wider front to back across its medial facet than L21306. The anterior flanges on the distal radii are wide apart and not strongly developed, the posteromedial facet for the scaphoid at maximum flexion is poorly hollowed, the anterior facets for lunate and scaphoid and the posterior one for the lunate are, however, better marked, that part of the articular facet for the cuneiform which lies on the radius is quite wide, and the distal end as a whole is swollen in side view. The articular surfaces of the metacarpal proximally do not fill the whole available area at the top of the bone, and the edge of the magnumtrapezoid facet does not have a single, clearly angled anteromedial corner. Distally there are poor hollows on the anterior surface above the condyles. The outer edges of the condyles are nearly parallel to one another.

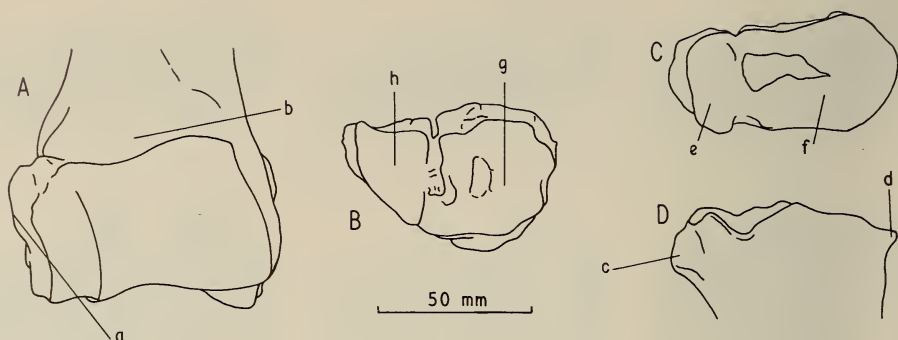


Fig. 13. Limb bones of *Simatherium demissum*, all shown as of the right side. A. Anterior view of distal humerus L41704. B. Proximal articular surface of metacarpal L41704. C. Proximal articular surface of radius L21306. D. Anterior view of same radius.

Anterior sides of B and C towards the base of the illustration.
 a = ridge behind hollow for lateral humero-radial ligament, b = coronoid fossa, c = lateral tubercle, d = medial rim of medial facet, e = lateral facet, f = medial facet, g = magnum-trapezoid facet, h = unciform facet.

Measurements

Measurements on the three best preserved skulls are:

	L45001	L30174	L30175
Total length of horn-core	299	292	348
Anteroposterior diameter at base of horn-core	74,8	59,6	70,0
Lateromedial diameter at base of horn-core	58,2	50,4	64,5
Minimum width across lateral sides of horn pedicels	187	—	192
Width across lateral edges of supraorbital foramina	90,4	—	—
Minimum width across temporal lines on skull roof	63,5	—	66,5
Skull width across mastoids behind external auditory meati	—	170	—
Occipital height from dorsal edge of foramen magnum	61,4	—	—
Width across anterior tuberosities of basi-occipital	22,6	28,8	23,0
Width across posterior tuberosities of basi-occipital	60,9	c. 64,0	48,5

Tooth measurements of these and other specimens in middle wear are given in Table 2.

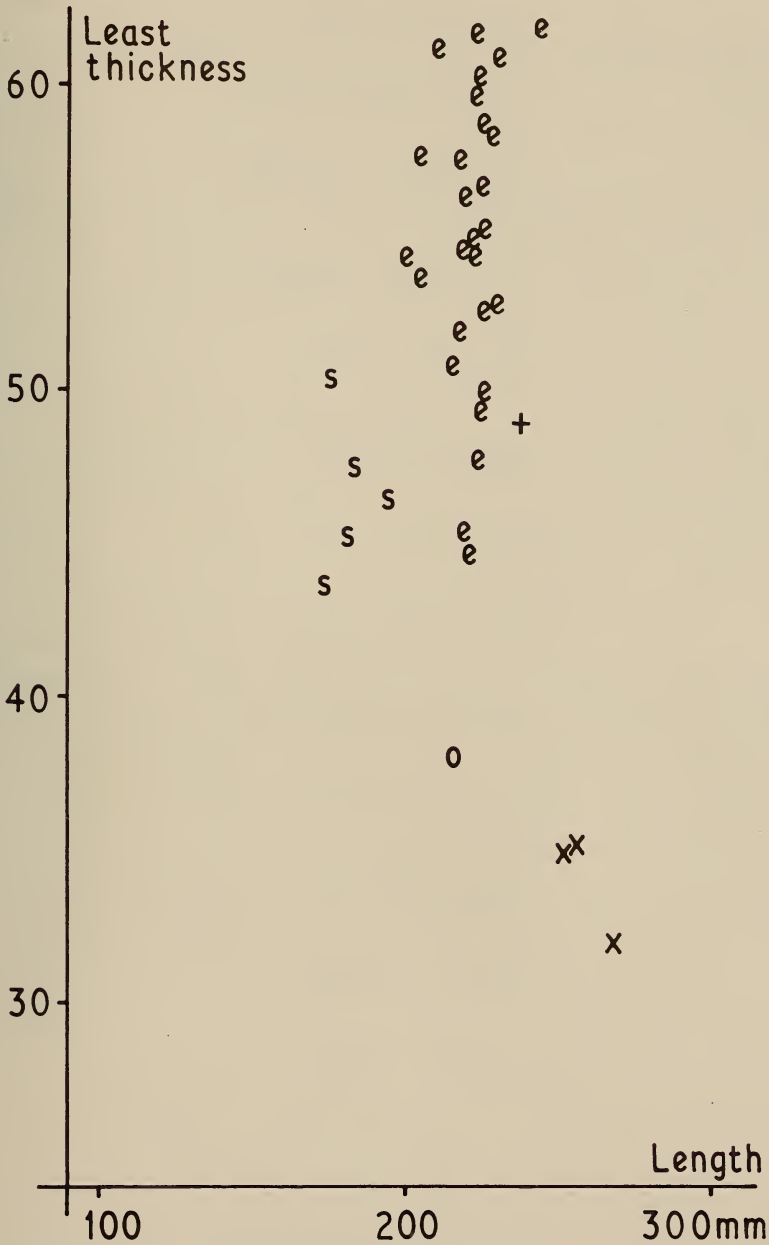


Fig. 14. Proportions of bovine metacarpals. X = E Quarry Langebaanweg, e = *Pelorovis ?antiquus* from Elandsfontein, S = extant *Syncerus caffer*, O = *S. acoelotus* BK 1952.218 from upper Bed II Olduvai Gorge, at present in Nairobi, + = *Pelorovis oldowayensis* associated skeleton from upper Bed II Olduvai Gorge.

TABLE 2
Measurements of bovine dentitions.

	L1843	L1843	L23400	L25861	L25861	L28328	L30175	L32609	L33841	L41709	L41736	L45001	L46073
	left	right	right	right	right	left	right	left	right	left	left	left	left
Upper length M1-M3	—	—	—	c. 97,2	105,7	—	82,6	92,8	c. 91,0	91,1	92,7	100,9	92,4
Upper length M2	—	—	† 28,3	34,9	33,2	28,2	29,6	28,6	29,2	27,9	32,3	31,2	31,2
Upper length M3	—	—	31,9	34,3	43,3	39,6	30,6	38,3	—	38,5	38,7	42,1	37,9
Upper length P2-P4	*67,8	*66,7	—	—	59,1	—	—	58,0	—	—	—	63,2	—
Upper length P2	*20,6	*14,4	18,8	23,9	17,8	—	—	15,5	17,4	—	—	18,5	—
Upper length P4	*24,1	*32,5	18,1	21,3	22,8	†21,2	19,5	22,2	21,5	21,2	19,6	23,7	19,4
Ramus depth below P ₂	—	—	—	—	40,0	—	—	—	—	37,0	37,4	37,3	—
Ramus depth below M ₁	—	—	—	—	46,7	—	—	—	—	46,0	47,4	c 44,0	—
Ramus depth below M ₃	—	—	—	—	65,4	—	—	—	—	—	61,6	51,6	—

L45001 occlusal length left M² = 33,7, right P⁴ = 20,5

* = deciduous dentition

† = right

‡ = left

Comparisons

Simatherium demissum is obviously similar to other African and Eurasian bovines of Miocene and Pliocene age, and comparisons must be made with the following forms:

Leptobos syrticus Petrocchi, 1956, from Sahabi. It is a primitive species but its generic attribution seems reasonable.

Parabos Arambourg & Piveteau, 1929, containing one or more species from the Ruscinian of France. Among these are the boselaphine-like *P. cordieri* Christol (Gervais), 1852, from Montpellier and *P. boodon* (Gervais), 1853, from Perpignan, generally considered to be a later site (Guérin 1975). In Europe *Parabos* predates *Leptobos*, but the primitive *L. syrticus* in North Africa is likely to be still older.

Proamphibos Pilgrim, 1939, containing one or more species from the Siwaliks. *P. lachrymans* Pilgrim (1939: 271) is the type species from the Tatrot Formation and *P. kashmiricus* Pilgrim (1939: 278) is apparently a more advanced *Hemibos*-like species, either contemporaneous or later. *Simatherium demissum* will not be compared with *P. kashmiricus*.

Ugandax gautieri Cooke & Coryndon, 1970, from deposits of unknown age in the Kazinga Channel of the Kairo Formation.

An unnamed species of *Ugandax* from the Hadar Formation.

Simatherium kohllarseni from Laetoli.

Simatherium demissum differs from *Leptobos syrticus* by being slightly smaller, its horn-core cross-section less clearly triangular (it has more expansion on either side of the anterior keel), horn-cores less divergent, horn-cores curved backward, supraorbital pits wider apart, braincase roof more strongly angled (in the Sahabi bovine it is almost horizontal), less strong temporal ridges and less of a temporal fossa, occipital surface probably less low and wide and certainly with a less long top surface, mastoids smaller and without deep pit-like excavations dorsomedially, median vertical ridge on occipital, and basioccipital more triangularly shaped with a more definite valley between the posterior tuberosities, narrowing more abruptly in front of the posterior tuberosities, and with smaller anterior tuberosities. The two forms are similar only in having a strong anterior keel, dorsal orbital rims which project well and horn-core insertions above the back of the orbits. The last resemblance is certainly a character which is primitive in bovines. Most of the differences can be recognized as being primitive or advanced in one or other of the species, and one is aware of two bovine lineages showing different characters advancing at different rates. More advanced *Leptobos*, like *L. falconeri* and the European Villafranchian species, have an almost horizontal braincase roof and very strong temporal ridges, and it is clear that the Langebaanweg bovine cannot be assigned to *Leptobos*.

A cranium of *Parabos cordieri* and a cranium and skull of *P. boodon* (Depéret 1890, pl. 7 (fig. 4); Piveteau 1961: 1052 fig. 145) were examined in the Institut de Paléontologie, Paris, and some horn-cores of *P. cordieri* in Basle.

Simatherium demissum differs from the skull of *P. boodon* by its shorter horn-cores, anterior keel stronger and posterolateral keel weaker, horn-core cross-section not so clearly triangular in shape, horn-core divergence more strongly diminished distally (i.e. a more curved course in anterior view), horn-cores probably inserted closer behind the orbits, horn-cores curve slightly backward, frontals not raised between the horn-core bases, better marked temporal ridges, more development of a rugose raised area posteriorly on the braincase roof, occipital surface with a horizontal top edge, teeth probably larger, styles larger on upper molars, slightly more localized ribs on anterior parts of lateral walls of upper molars. It seems likely that the facial part of the *P. boodon* skull has been displaced downward and that this has reduced the apparent inclination of the horn-cores in profile. Originally they would have been more upright than in *S. demissum*.

The large cranium of *P. boodon* from Perpignan has horn-cores with no posterolateral keel at all, more strongly diminished distal divergence and a slight degree of backward curvature, flatter frontals, horn-cores set more closely to the orbits, better temporal ridges, braincase roof less slanted, and is thus less different from *Simatherium demissum* than is the complete skull. It is possible that its frontals' morphology is more representative of the species than that of the complete skull, and its horn-cores are more uprightly inserted than in the Langebaanweg bovine. The absence of a posterolateral keel is puzzling. The basioccipital is preserved on this specimen. It is unlike that of *S. demissum* by being wider anteriorly, not narrowing abruptly just in front of the posterior tuberosities, not having a narrow and deep central groove between them, and not having a central longitudinal ridge.

The cranium of *Parabos cordieri* is well removed from resemblance to *S. demissum* by its smaller size, and horn-cores which are less divergent basally and less robust. It also has a more clearly triangular cross-section and sometimes a better marked posterolateral keel. It agrees with the South African species in having little compression of the horn-cores, horn-cores set widely apart and close above the orbits, temporal crests present, a rugose area at the back of the braincase roof, mastoids not very large, and basioccipital narrowed immediately in front of the posterior tuberosities. The Basle examples have a low inclination of the horn-cores.

It is interesting that the teeth of *Parabos* appear to have about the same level of brachyodonty and occlusal complexity as *S. demissum*.

One can see *Parabos cordieri* to *P. boodon* as a bovine lineage evolving in Europe before the appearance there of *Leptobos* which displaced it. From the facts just given, one can sum up the differences of *Parabos* as a whole from *S. demissum*. *Parabos* has variable development of the posterolateral keel and generally an anterior keel, whereas *S. demissum* had already lost its supposed ancestral posterolateral keel, but has a strong anterior keel. Again, *S. demissum* has evolved horn-cores with strong basal divergence and distal recurvature. Their low inclination is matched only by the Basle example of *P. cordieri*. The

upper molars on the *Parabos* skull had evolved rather small styles but retained less localized anterolateral ribs than *S. demissum*. Such differences seem sufficient to show that *Parabos* must have been a different lineage, and this is compatible with the geographical circumstances.

Simatherium demissum differs from *Proamphibos lachrymans* as from *Leptobos syrticus* and *Parabos* by its shorter and more robust horn-cores, their less regularly triangular cross-section, greater basal divergence, and a more curved course in anterior view. These can all be considered advanced characters. Other differences are horn-cores inserted less widely apart in *S. demissum*, supra-orbital pits less wide apart, more projection of the orbital rims, horn-core insertions probably less far behind the orbits, occipital surface lower and wider, presence of a central longitudinal ridge on the basioccipital, and smaller anterior tuberosities. *S. demissum* agrees with *P. lachrymans* in the degree of mediolateral compression and a strong anterior keel on the horn-cores, in the inclination of the horn-cores in side view, and even in the slight swelling of the cross-section laterally to the anterior keel. It also agrees in the not very large mastoids and many cranial characters.

Simatherium demissum is more advanced than the *Ugandax gautieri* holotype by its larger size, horn-core insertions wider apart, horn-cores more divergent basally and with a more curved course, probably a shorter braincase and a more triangular basioccipital. It is more primitive in retention of a strong anterior keel, horn-core insertions closer to the orbits, a rugose area on the braincase at the top of the occipital, and smaller anterior tuberosities of the basioccipital. Other differences lie in its transverse constriction of the basioccipital immediately in front of the posterior tuberosities, the valley between the posterior tuberosities of the basioccipital, the central longitudinal ridge less pronounced on the basioccipital and the smaller mastoids. It is similar in its short to moderate horn-core length, degree of mediolateral compression, lack of a very orderly triangular cross-section, inclination of the insertions, and most of the other cranial characters. Thomas (1979b, pl. 2 (figs 1, 3, 5)) has identified bovine teeth at Lukeino as *Ugandax* cf. *gautieri*. They are very similar to those from 'E' Quarry but a little smaller.

The Afar *Ugandax* is generally a more advanced species than *U. gautieri*. It may have occurred later, although the time level of *U. gautieri* is unknown. *S. demissum* has many differences from the Afar *Ugandax* sp. It is more primitive in its horn-cores with a stronger anterior keel, usually more backwardly curved, the horn insertions closer behind the orbits, the braincase less low and wide, the smaller anterior tuberosities of the basioccipital, and the occlusal surface of the cheek teeth less complicated both in the outline of the central cavities and in the absence of constrictions across the lateral lobes of the lower molars. It is more advanced in the greater divergence of its horn-cores, their insertions being wider apart, the occipital with perhaps a straighter top edge, its longer molars (Fig. 15), the relatively shorter premolar rows (Fig. 16) and in the metaconids of P₃ and P₄ perhaps less diagonally slanted backwards. Other

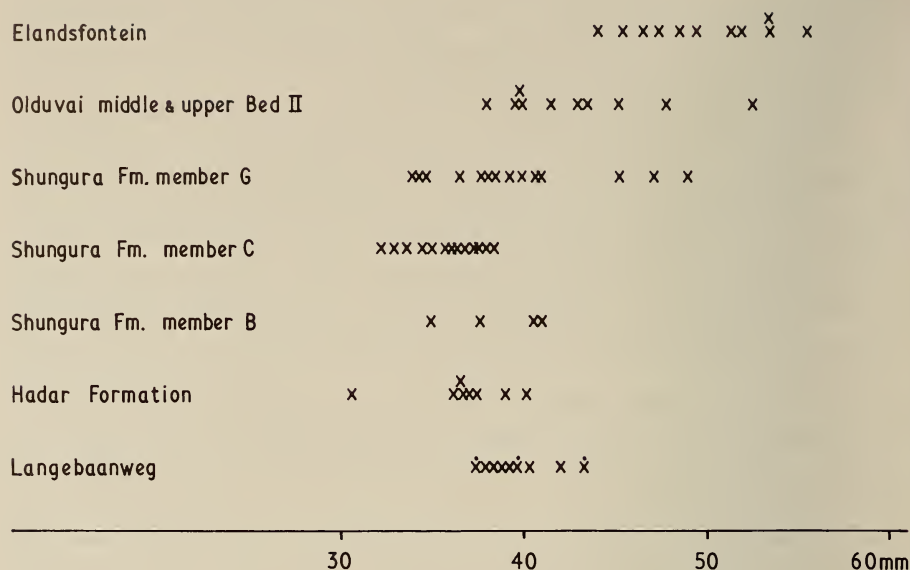


Fig. 15. Occlusal length of bovine M_3 s. Dotted Langebaanweg readings are QSM, others are PPM. Elandsfontein sample is *Pelorovis ?antiquus*. The four largest readings for Olduvai and for Shungura member G are likely to be *P. oldowayensis*. Other Olduvai and Omo readings are *Syncerus*, and Hadar Formation ones are *Ugandax* sp. Not until Olduvai does *Syncerus* become comparable in length with the Langebaanweg bovine.

differences from the Afar species are the strong projection of the orbital rims, more of a median vertical ridge on the occipital, smaller mastoids, and a longer basioccipital with a central longitudinal ridge and a valley between its posterior tuberosities. A comparison of skull measurements between the Afar and 'E' Quarry bovines is shown in Figure 17.

Simatherium demissum differs from the Berlin *S. kohllarseni* by its smaller size, anterior keel, horn-cores inserted less extremely widely apart, lower inclination of the horn insertions, less divergent horn-cores, horn-cores with a slight backward curvature which is not confined to the basal sector, a less irregular surface of the horn-core, no consistent shallow longitudinal groove running along the horn-core, frontals not transversely arched between the horn-core bases, clearer temporal ridges and no temporal fossa below overhanging horn-core insertions. It differs from the more recently recovered example by an anterior keel, lower inclination of horn-cores, less divergent horn-cores, horn-cores with slight backward curvature, a less irregular surface of the horn-core and no deep longitudinal grooves anteroventrally, more of a median vertical occipital ridge, and a smaller mastoid.

It is similar to both these Tanzanian fossils in its short robust horn-cores, without compression, loss of a triangular cross-section, horn-cores inserted

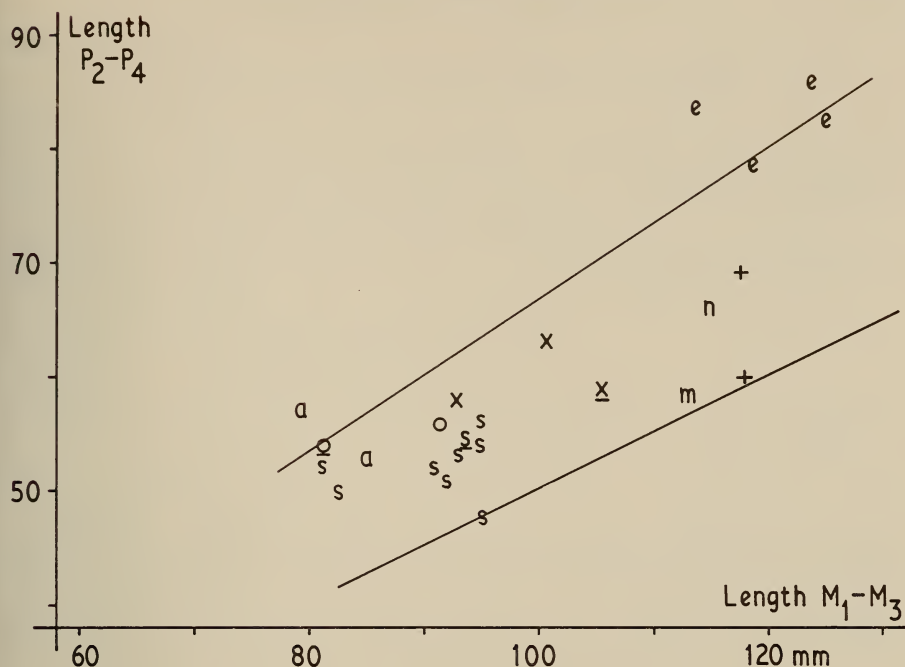


Fig. 16. Occlusal lengths of lower premolar and molar rows in Bovini. X = bed 3aN Langebaanweg, \underline{X} = QSM Langebaanweg, e = *Pelorovis ?antiquus* from Elandsfontein, n = *P. antiquus* from Naivasha, Kenya, + = *P. oldowayensis* from upper Bed II Olduvai Gorge, S = extant *Syncerus caffer*, \underline{S} = *S. caffer* from latest Pleistocene Kibish Formation, Omo (see Gentry & Gentry 1978: 308-322 for this and other bovine fossils), O = *S. acoelotus* from upper Bed II Olduvai Gorge, Q = *S. ?acoelotus* from Shungura Formation member G, m = *Syncerus* sp. from Melkbos, a = *Ugandax* sp. from Hadar Formation. Lower diagonal line = 50 per cent, upper one = 66,7 per cent as in Figure 3.

widely apart, the slope of the braincase, temporal ridges, a raised area on the brain roof at the top of the occipital, occipital proportions similar, a flat-topped occipital with side edges formed by the nuchal crests, basioccipital with a central longitudinal ridge in the area just behind the level of the anterior tuberosities, and a very deep, short groove between the posterior tuberosities.

A *Simatherium* such as the Langebaanweg species could be ancestral to the Laetoli one. Nearly all its differences from the Laetoli examples can be thought of as more primitive, and this contrasts with the comparisons previously made with other bovines. It is interesting that at Langebaanweg the horn-core insertions are more inclined. Either this character is primitive for the genus or it could be an indication of regional specialization at an early time level.

Tribe Reduncini

Kobus A. Smith, 1840

Type species

Kobus ellipsiprymnus (Ogilby, 1833).

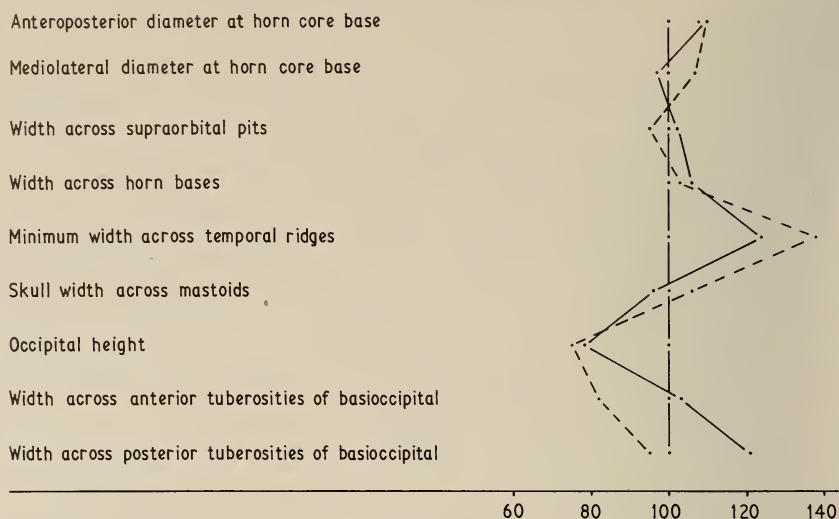


Fig. 17. Percentage diagram of skull measurements in Bovini. The standard line at 100 per cent is the holotype of *Proamphibos lachrymans* (M 26576, cast) and readings on other lines are expressed as percentages of their values on the standard line. The second continuous line is the holotype of *Simatherium demissum*, and the dashed line is *Ugandax* sp. AL 194-1 from the Hadar Formation. The African forms are wider across the temporal ridges, have lower occipitals, and have basioccipitals with relatively narrow anterior tuberosities.

Generic diagnosis

Larger sized reduncines; horn-cores usually long, their bases sometimes curving backward instead of being concave anteriorly, usually with a flattened lateral surface but no tendency towards a flattened posteromedial surface; frontals sometimes with a small system of internal sinuses.

Remarks

A majority of the *Kobus*-like horn-cores and possibly the back of a reduncine cranium from 'E' Quarry, Langebaanweg, belong to a short-horned species which is given a new name below. Two problems surround these remains. A major one is that dentitions apparently associated with these horn-cores are very unlike other known reduncines. If the association could be proved beyond question, i.e. by the recovery of a skull with both horn-cores and teeth, then a new generic name would be needed for this species. Meanwhile it is put into *Kobus*. A lesser problem is that the two most completely preserved crania with horn-cores show a small suite of character differences from the other horn-cores and cranium. They may represent another species and are described under the heading *Kobus* sp. 2.

Kobus subdolos sp. nov.

Figs 18-20.

Holotype

L30878—right horn-core with part of frontal, dorsal part of orbital rim and supraorbital pit (Fig. 18).

Referred material

The main specimens assigned to this species are as follows:

From bed 3aS:

L41387—frontlet with nearly complete horn-cores. Index $48,7 \times 41,0$, minimum width across lateral sides of horn pedicels 92,9, width across lateral edges of supraorbital foramina 45,7

L40248—left horn-core, index $43,8 \times 37,5$; same individual as right horn-core L40371

L40049—right horn-core, index $41,5 \times 37,0$

L40051—left horn-core, index $39,2 \times 33,6$

Probably from bed 3aS, but a few possibly from QSM:

L1847, L2609, L6076, L10672—left horn-cores, the second and fourth with indexes $50,2 \times 41,2$ and $43,5 \times 35,6$

L2611, L2612—right horn-cores, indexes $46,5 \times 35,9$ and $41,4 \times 36,6$

L2604, a reduncine cranium preserved only from a level behind the horn bases, may be conspecific with the horn-cores (Fig. 19). Its measurements are:

Maximum braincase width	80,2
Minimum width across temporal lines on skull roof	28,1
Skull width across mastoids behind external auditory meatus	92,3
Occipital height from dorsal edge of foramen magnum	44,0
Width across anterior tuberosities of basioccipital	31,0
Width across posterior tuberosities of basioccipital	35,9

From bed 3aN:

L40726—left horn-core, index $40,2 \times 33,0$; same individual as right horn-core L40728

L40870—left horn-core, same individual as right horn-core L40872, index *c.* $50,5 \times 43,0$

L46062—right and left horn-cores, index $50,3 \times 46,0$, length *c.* 190

L30879—index $46,7 \times 40,3$, L41754 $45,7 \times 39,8$, L46044 $41,1 \times 36,3$, L46045 $43,0 \times 40,3$, L46048, L46060 $47,7 \times 41,2$ and length 197, L46069 $50,9 \times 43,0$ and length 159—left horn-cores

L30029—index $47,7 \times 36,1$, L30878 $44,4 \times 37,6$, L33383 $47,7 \times 40,0$, L33746 $43,3 \times 35,0$, L40873 $46,0 \times 32,7$, L41755 $42,6 \times 36,5$, L46049 $39,7 \times 35,6$, L46070 $44,4 \times 36,6$ and length 172, L46071 $54,4 \times 46,3$ and length 178—right horn-cores

L32163—partial occipital surface and basioccipital

Locality

The holotype comes from bed 3aN of the PPM. The provenance of other specimens has already been given, and it can be seen that the species is not definitely known from the QSM.



Fig. 18. *Kobus subdolos*. L30878, holotype. Right horn-core in lateral and anterior views. Scale = 25 mm.



Fig. 19. *Kobus subdolos*. L2604, cranium. From the left: occipital view, lateral view, ventral view. Scale = 25 mm.

Diagnosis

An antelope about the size of *Kobus kob* or *K. leche*. Horn-cores short, little compressed mediolaterally, with a flattened lateral surface, their widest mediolateral diameter lying rather anteriorly and the cross-section narrowing behind this level to a posterolateral edge which does not quite assume the form of a keel. Deep grooves run longitudinally just medial to this posterior edge. A minority of horn-cores show transverse ridges which are V-shaped and close together. Horn-cores inserted above the orbits, at a low inclination and close together, not very divergent and with divergence perhaps lessening distally. They show little curvature but the tips curve forward slightly. Anterior edge of horn pedicels sometimes set uprightly in profile and thus at an angle to the anterior edge of the horn-core proper. Postcornual fossa small and deep, frontals little raised between horn-core bases, supraorbital pits large.

Etymology

The specific name taken from the Latin *subdolus*, is somewhat deceitful, and refers to the species not having teeth which are clearly reduncine.

Remarks

The most striking features of *Kobus subdolus* horn-cores is that they are so short. Transverse ridges may be seen on 5 out of 17 left horn-cores and 3 out of 14 right ones. The tendency towards an upright anterior edge of the horn pedicel can be seen in 5 among 16 and 6 among 15 right horn-cores. It is possible that those from bed 3aN are larger than from 3aS (Fig. 20), but the difference is not statistically significant, even if the two 3aN horn-cores of '*Kobus* sp. 2' are, indeed, a separate species.

The reduncine cranium L2604 is presumably conspecific with the horn-cores. There is no central indentation in the parietofrontals suture as it passes across the top of the skull, the temporal lines approach fairly closely posteriorly, the braincase widens posteriorly, its roof is inclined in profile and not curved downward posteriorly, the nuchal crests are not very strongly developed, the occipital surface is fairly high and narrow and faces backward, its edge is not evenly rounded, the median vertical ridge of the occipital appears to have been present and had shallow depressions flanking it dorsally, the fairly small mastoids lie mostly within the bounds of the occipital surface and do not have a pronounced dorsal or ventral rim, the anterior tuberosities of the basioccipital are very large, longitudinal ridges pass backward from the anterior tuberosities and converge posteriorly (giving the appearance of a transverse constriction across the centre of the basioccipital), the posterior tuberosities take the form of posterolaterally directed transverse ridges, and the auditory bulla is large and inflated. The large size of the auditory bullae is noteworthy. Another fragmentary occipital surface with part of the basioccipital, L32163, appears to be conspecific.

One or two limb bones from 'E' Quarry are identified as possibly reduncine. L30392 from bed 3aN includes a distal right humerus with much of its shaft

and an associated proximal right radius and reduncine dental remains. Two distal humeri likely to be conspecific are L31937B and L32629 from bed 3aN and two further proximal radii are L31937C from bed 3aN and L24932 from the QSM (Fig. 21). The humeri show the following characters:

1. The distal part of the lateral surface is wide behind the ridge bounding the hollow for the lateral humeroradial ligament.
2. The ridge on the distal part of the lateral side for the origin of the extensor carpi radialis is marked, especially in L31937B.
3. The coronoid fossa is deep in L30392 and L32629 but not in L31937B.
4. In L31937B and L32629 the condyles are slanted but this is not true for L30392.
5. The medial groove on the condyles is deep in L30392 and L32629 but shallow in L31937B.
6. The hollow for the lateral humeroradial ligament is deep in L30392 and L32629 but shallow in L31937B.
7. The medial condyle passes high into the coronoid fossa in L30392 and L32629 but this is less clear in L31937B.

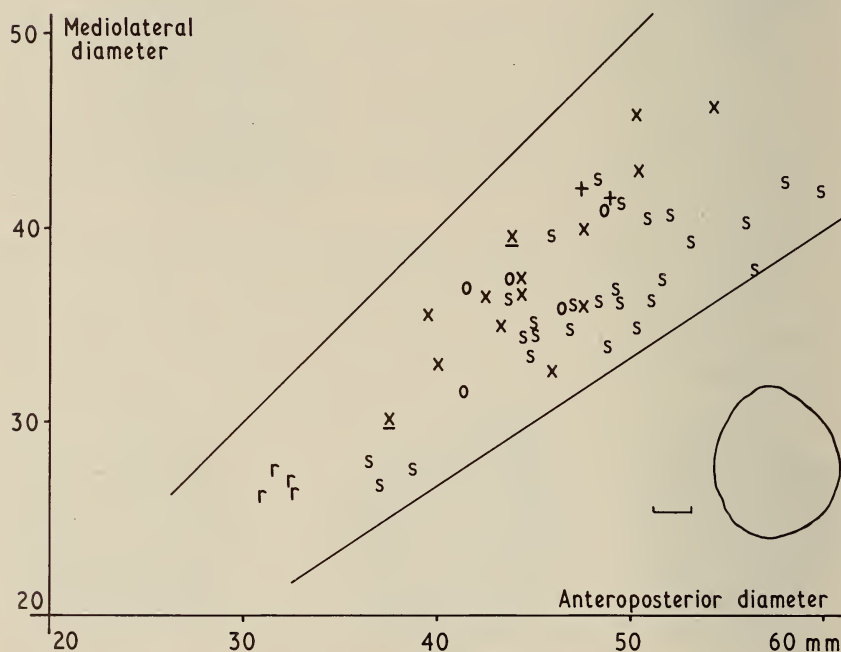


Fig. 20. Basal diameters of reduncine horn-cores. O = bed 3aS Langebaanweg, X = bed 3aN, \bar{X} = *Kobus* sp. 2, + = *Kobus* sp. from Sahabi, r = *K. porrecticornis* from Baard's Quarry, S = *K. sigmoidalis* from members C-F inclusive of the Shungura Formation. Upper diagonal line = 100%, lower one = 66,7% as in Figure 3. A cross-section of the right horn-core L2612 is shown, taken 20,7 mm above its base, with lateral side to the left and anterior side to the base. Scale = 10 mm.

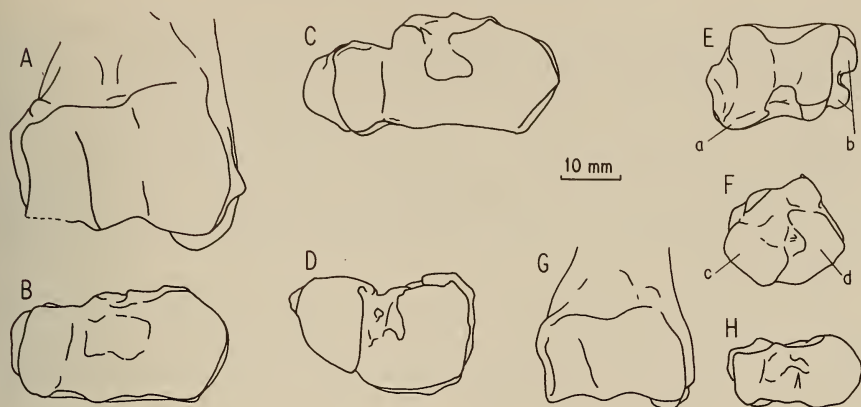


Fig. 21. Limb bones of Reduncini, Alcelaphini and Neotragini, all shown as of the right side.

Anterior sides of proximal and distal views are towards the base of the illustration.

A. Anterior view of distal reduncine humerus L24932. B. Proximal articular surface of associated radius L24932. C. Proximal articular surface of alcelaphine radius L41482. D. Proximal articular surface of associated metacarpal L41482. E. Distal articular surface of neotragine tibia L41684. F. Proximal articular surface of associated metatarsal L41684. G. Anterior view of distal neotragine humerus L40787. H. Proximal articular surface of neotragine radius L40088 with part of its back edge taken from L40021.

a = medial malleolus, b = fibula facets, c = main facet for naviculocuboid, d = main facet for ectocuneiform.

For the first four characters two or all three of the humeri are unlike alcelaphines, but for the last three characters L30392 and L32629 resemble them. None of the characters is definitely unlike later Reduncini, and although the second and third could be held to resemble Tragelaphini, the last three do not agree very well with that tribe.

Most characters of the proximal radii are unlike Alcelaphini: the lateral facet is broader and longer (not in L31937C), not pointed anteriorly, and its posterior edge is not stepped forward from the level of the back edge of the medial facet. The lateral tubercle is small and low. The indent in the back edge of the medial facet is less deep than in Alcelaphini, and the anteromedial part of that facet is more extensive in L30392 (but not in L31937C or L24932) than in Alcelaphini. It is interesting that there is no medial rim on the medial facet—unlike later Reduncini or Tragelaphini.

Comparisons

The Langebaanweg fossils agree well with a frontlet and three horn-core pieces from Sahabi, now in Rome. The Sahabi horn-cores are about the same size, not very compressed mediolaterally, with some flattening of the lateral surface, hardly any backward curvature basally but with some upward curvature towards the tips, and their widest mediolateral diameter lying rather anteriorly. The supraorbital pits are close together and may have been rather large, the dorsal part of the orbital rim is strongly projecting, and the parieto-

frontals suture is transversely straight across the top of the skull. The Sahabi horn-cores although short are less short than the Langebaanweg ones and they diverge more. There are no transverse ridges on the horn-cores and no angling of the front edge of the pedicel on the line of the horn-core proper, but the condition of both these characters is variable in the Langebaanweg fossils.

The cast of a right horn-core, BM(NH) M 8200, from Wadi Natrun is a little smaller than the Sahabi and Langebaanweg ones but similarly rather short, little compressed and with its widest transverse diameter lying at rather an anterior level.

Measurements on the Sahabi frontlet are: horn-core index $47,4 \times 42,0$, horn-core length 218, minimum width across lateral sides of horn pedicels *c.* 102, and width across supraorbital pits probably near 50. The basal index for another Sahabi horn-core is $49,0 \times 41,5$, and for the Wadi Natrun cast $38,8 \times 30,6$. The length of the Wadi Natrun cast is *c.* 150.

Kobus subdolus is unlike the early reduncine *K. porrecticornis* of the middle Siwaliks by its larger size, shorter and less divergent horn-cores which are without backward curvature and are inserted at a lower inclination, and by its occasional possession of transverse ridges. *K. porrecticornis* is discussed again in the account of Baard's Quarry fossils.

Compared with *Redunca darti* of Makapansgat Limeworks, the Langebaanweg species shows closer insertions of the horn-cores and probably closer supraorbital pits as well, more oblique insertions, the tendency to have a front edge of the pedicel at an angle to the front edge of the horn-core, and horn-cores with a completely different cross-sectional shape. This last feature arises from the horn-cores having a flattened lateral surface, narrowing posteriorly in cross-section so that there is an approach to having a posterior keel, having no hollowing or flattening posteriorly or posteromedially at the base, and being slightly compressed mediolaterally. The Langebaanweg species also differs in having no central indentation of the parietofrontals suture, a less pronounced ventral rim of the mastoid, and possibly better marked hollows flanking the median vertical ridge of the occipital surface. It must be a different lineage from *R. darti*.

Kobus subdolus differs from undescribed reduncine crania and horn-cores from the Hadar Formation, Afar, by its short horn-cores with flattened lateral surfaces and a slight degree of mediolateral compression, less narrow mastoids, larger bullae, larger anterior tuberosities of the basioccipital, less narrow posterior tuberosities of the basioccipital, and no anterior indentation of the parietofrontals suture. It is clear that the Afar species is a different lineage not very closely related to the Langebaanweg form.

Compared with Siwaliks reduncines from the Pinjor Formation which may be assigned to *Sivacobus palaeindicus* (BM(NH) 17437, 39559, M 487, and M 2402 which Gentry & Gentry (1978: 337) discussed), *Kobus subdolus* shows horn-cores with a flattened lateral surface, more mediolateral compression, their widest mediolateral diameter lying more anteriorly, and more of an

approach to a posterolateral keel. The cranium L2604 also has weaker temporal ridges, no central indentation in the parietofrontals suture, not such pronounced posterior widening of the braincase, and not such a strong median vertical ridge on the occipital.

Despite a number of differences such as shortness and less mediolateral compression (Fig. 20), the 'E' Quarry horn-cores recall the species *Kobus sigmoidalis* and *K. ancystrocera* from the Shungura Formation, Omo, by their cross-section with a flattened lateral surface and an approach to a posterolateral keel, the very low insertion angle in side view, and the manner in which the front of the pedicel is angled on the axis of the horn-core proper. The two Omo species seem to belong to a 'modern' group of reduncines related to the living waterbuck and Central African lechwe and to living and fossil kob. On the Langebaanweg cranium L2604 the occipital is higher and narrower than in the Shungura species, which one could imagine to be a primitive character befitting a more ancient species. However, the evidence of the reduncine teeth at Langebaanweg must be considered before making a final assessment of likely phylogenies.

The question of reduncine teeth at Langebaanweg

In 1975 the most northerly exposures of bed 3aN were excavated and among the bovid horn-cores there was the following representation of individuals: *Tragelaphus* two, *Mesembriportax* one, *Simatherium* three, *Kobus* six, *Damalacra* one. No teeth were found which were unquestionably reduncine in appearance, despite the predominance of *Kobus* horn-cores, but the commonest group of teeth, coming from at least seven individuals, appeared to be most like *Tragelaphini*. They agreed with teeth found in earlier years in 'E' Quarry and assigned to *Tragelaphini*, and showed the following characters:

1. Dentition rather low crowned . . . like *Tragelaphini*, also a primitive character
2. Hardly any development of ribs between the styles on the lateral walls of the upper molars . . . like *Tragelaphini*
3. No basal pillars on upper molars and only tiny ones on lowers . . . like *Tragelaphini*
4. Anteromedial lobe of upper molars is not connected in early wear to the junction of the posteromedial with the anterolateral lobes . . . a primitive character
5. Premolar row moderately long . . . intermediate between Reduncini and *Tragelaphini* (Fig. 22)
6. P³ and especially P² large in comparison with P⁴ . . . like *Tragelaphini*
7. Central cavities of P³ and P⁴ sited rather anteriorly . . . like *Tragelaphini*, also a primitive character

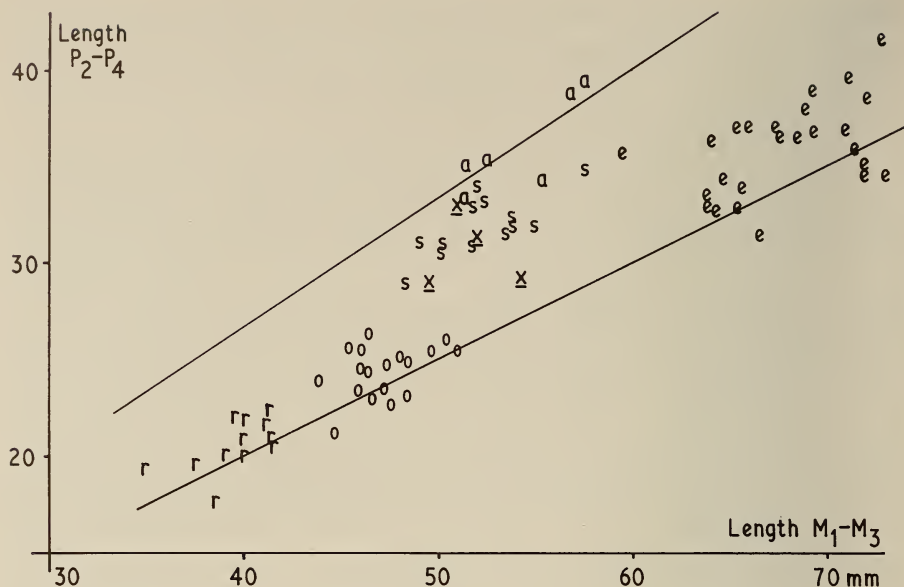


Fig. 22. Occlusal lengths of lower premolar and molar rows in Reduncini and Tragelaphini. \bar{X} = bed 3aN Langebaanweg, a = extant *Tragelaphus angasi*, S = extant *T. spekei*, e = extant *Kobus ellipsiprymnus*, O = extant *K. kob*, r = extant *Redunca redunca*. Lower diagonal line = 50%, upper one = 66,7% as in Figure 3.

- | | |
|---------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------|
| 8. Small goat folds present on lower molars, presumably not a primitive character | a tendency towards Reduncini |
| 9. Medial walls of lower molars with slight outbowings only | like Tragelaphini—flatter than in <i>T. spekei</i> and <i>buxtoni</i> * |
| 10. Lateral lobes pointed but not narrowed in their lateral part | like Tragelaphini |
| 11. Medial wall of back lobe of M_3 set more laterally than medial wall of anterior lobes | like Reduncini |
| 12. Hypoconid of P_4 often not projecting laterally and never with a deep valley in front of it | like Tragelaphini, also a primitive character |
| 13. Paraconid-metaconid on P_4 usually not fused but metaconid growing forward | like Tragelaphini and <i>Redunca arundinum</i> |
| 14. A backwardly directed flange is usually present on P_4 metaconid | frequent in Tragelaphini |

* Extant *Tragelaphus spekei* and *buxtoni* have less flattened walls than *T. imberbis*, *strepsiceros* and *eurycerus* and *Taurotragus oryx*. *Tragelaphus angasi* and *scriptus* are probably intermediate.

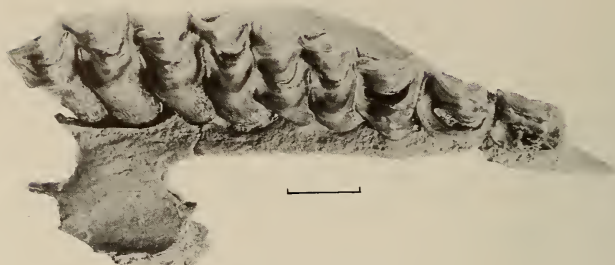


Fig. 23. *Kobus subdolos*. L32850, occlusal view of right upper tooth row. Scale = 10 mm.

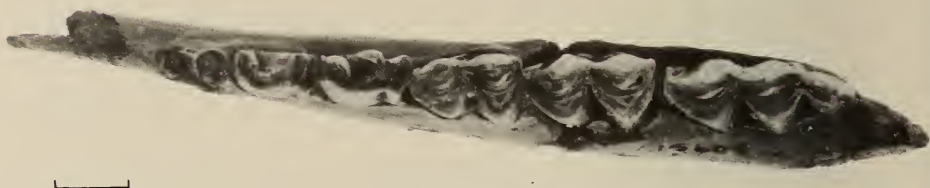


Fig. 24. *Kobus subdolos*. L15605, occlusal view of left lower dentition. Scale = 10 mm.



Fig. 25. *Kobus subdolos*. L32850, L46067, lateral views of right mandibles. Scale = 10 mm.

Measurements for these teeth are given in Table 3 and they are illustrated in Figures 23–25. Readings for occlusal length and metastylid crown height in M_{3s} in early middle wear are:

L10551	right	$21,7 \times 12,5$	L31171	right	$c. 23,2 \times 14,0$
L20906	left	$23,4 \times 14,1$	L31916	left	$25,6 \times 17,4$

Other readings of occlusal length are:

L1843C left P_4 13,3 probably PPM, L10292 left dP_4 18,4 3aS or QSM.

Some characters not mentioned in the list do not show a clear trend towards one tribe rather than the other. For example, the anterior part of the lateral wall of P_4 sometimes bends round to become almost transversely oriented as in Reduncini, and sometimes remains mainly anteroposteriorly directed as in Tragelaphini. Again, some of the mandibles, e.g. L32850, are rather shallow anteriorly while others, e.g. L30392, are deeper, and it is not possible to say which condition is more like Tragelaphini and which is more like Reduncini.

For assessment of the tribal affinity of these teeth, much depends on the 'direction' of their evolution. In some cases, for example the first character in the list, one can feel confident that the brachyodonty of the cheek teeth is not only more like Tragelaphini than Reduncini, but also that it is more primitive than the high-crowned teeth of later Reduncini. In other cases it is harder to guess whether or not a condition is primitive without a prior knowledge of phylogeny.

The only indication of changes within the span of 'E' Quarry deposits is that the measured mandible and maxilla from the QSM have relatively small molar teeth, but one cannot know that larger samples would validate this difference. The tooth assemblage cannot be assigned satisfactorily to more than one species and if this species should be *Kobus subdolus*, one tooth only (p. 223) is left to go with *Tragelaphus*.

It is possible that these teeth show an early stage in the evolution of reduncine characters. This implies that Reduncini had ancestors with tragelaphine-like teeth, and that at Langebaanweg recognizably reduncine teeth had not yet evolved. Hitherto it has seemed likely that Reduncini would have evolved from boselaphine ancestors (Gentry 1978b: 567) although Pilgrim (1939: 21) and Simpson (1945: 272) were not definite about their boodont affinities. In the Siwaliks succession one finds small boselaphines (*Protragocerus gluten*, *Miotragocerus gradiens*) in the Chinji Formation, and then in the Nagri and Dhok Pathan Formations boselaphines of varying but generally larger size—*Pachyportax latidens*, *Selenoportax vexillarius*, *Miotragocerus punjabicus* and *Tragoportax salmontanus*. Towards the top of the Dhok Pathan Formation, or shortly afterwards, these overlap or give way to the early bovine *Proamphibos*, Reduncini, and the supposed hippotragine teeth assigned to *Sivatragus*. Undoubted boselaphines are rare in the Tatrot Formation (Pilgrim 1939: 6). In this succession it is easy to visualize the derivation of Tatrot reduncine teeth from boselaphine ancestors without the need for any diversion towards a tragelaphine-like morphology. Such a derivation clashes with that favoured by the Langebaan-

weg teeth in which characters 2, 3, 6, 9, 13 and perhaps 10 and 14 are unlike either reduncines or early boselaphines.

A certain number of fossil reduncine teeth were examined for signs of descent from Langebaanweg-like ancestors, but the results were not conclusive. Among pre-Pinjar fossils from the Siwaliks were BM(NH) M 34568 a cast of a palate B 815 with left P^2-M^3 and right P^3-M^3 (Pilgrim 1939: 107, fig. 11a); M 15372, part of a left mandible with M_2-M_3 and a fragment of M_1 (Pilgrim 1939, pl. 3 (fig. 13)); M 15385, various lower teeth; M 34569, a cast of part of a right mandible B 816 with P_2-P_4 (Pilgrim 1939: 119, fig. 11b). All come from the Hasnot-Tatrot area and the first three were believed to come from the Tatrot Formation. The last may be from deposits equivalent in age or slightly younger than the type Dhok Pathan Formation but this is not certain. They could belong to *Kobus porrecticornis*, a species known from horn-cores and first known to occur in the upper Dhok Pathan Formation (Thomas 1979b; Pilbeam *et al.* 1977: 687). (A left P_4 , M 15371 (Pilgrim 1939, fig. 11c), was earlier identified as reduncine but appears to be alcelaphine.) Other available reduncine fossils came from the middle of the Hadar Formation and from various parts of the Shungura Formation. The oldest reduncine teeth in Africa are from Lukeino and Mpesida, and these, too, could belong to *K. porrecticornis* or *K. aff. porrecticornis* (Thomas 1979b, pl. 1 (fig. 6), pl. 2 (figs 6-7)). Compared with living reduncines, these fossils showed that earlier members of the tribe had lower crowned teeth, smaller basal pillars, less strong ribs on the lateral walls of the upper molars, smaller goat folds and less narrowed lateral lobes on the lower molars, longer premolar rows and the entoconulid more distinct from the entoconid on the back of P_4 . There is also interesting evidence for a closer approach of paraconid and metaconid on P_4 . The lower part of the paraconid on the nearly unworn P_3 and P_4 of B 816 has a flange growing backwards. Afar P_4 s have paraconid and metaconid growing very close to one another (e.g. AL 153-3, AL 156-1A and AL 167-5) and a Shungura example, L2-46B, shows a flange on the metaconid of P_4 . Among later reduncines only *Redunca arundinum* and ontogenetically older *Kobus ellipsiprymnus* have an approach to fusion of paraconid and metaconid. In a sample of 31 *Redunca arundinum* P_4 s only 15 show close approach or fusion of paraconid and metaconid. They effect this more by forward growth of the metaconid than by backward growth of the paraconid, but in the Afar examples it looks as if backward growth of the paraconid is the more important.

None of these characters is taken so far as to demand descent from a form with teeth similar to those at Langebaanweg. Even the approach or fusion of paraconid and metaconid on P_4 can evolve in boselaphines and its appearance in some reduncines need not imply affinity with the Langebaanweg teeth.

Reduncine phylogeny

Returning to the question of possible phylogenies, one sees that Langebaanweg, Sahabi, and Wadi Natrun have one or more reduncine species with horn-

cores which would be good structural ancestors for modern *Kobus* and the extinct Shungura species *K. sigmoidalis* and *K. ancystrocera*. However, tooth morphology suggests that *K. porrecticornis* or *K. aff. porrecticornis* may be a better ancestor. Its teeth are known back to Lukeino and Mpesida and perhaps to the upper part of the Dhok Pathan Formation, so Langebaanweg could be earlier than these sites, or its reduncine retained primitive teeth late in geological time, or its reduncine teeth have been incorrectly identified.

The most interesting aspect of the Langebaanweg reduncine fossils is that they are more like the aegodont *Damalacra* than the boodonts *Tragelaphus* sp., *Mesembriportax acrae* or *Simatherium demissum*. This is shown in their narrower skull proportions, absence of keels other than the trace of a posterolateral one, close insertions of the horn-cores, poor basal divergence of the horn-cores, deep postcornual fossa, inclined cranial roof, absence of strong temporal ridges, absence of a rugose area at the back of the braincase roof, and the good-sized anterior tuberosities of the basioccipital. Only in the teeth can even a few boodont characters be seen: basal pillars on the lower molars, retarded joining of the lobes of the upper molars in ontogeny, and the long premolar rows. However, poor development of ribs relative to styles on the upper molars and rather flat medial walls of the lower molars could be seen as aegodont characters. Some of the dentitions, e.g. L32850, show signs of transverse wear ridges across the dentine of the upper molars, and this too parallels caprines. One has to ask whether the Reduncini are properly to be considered as a boodont group, and what the evolutionary relationship is between those of the Siwaliks and of Langebaanweg, but for the present there seem to be no answers.

Kobus sp. 2

Figs 26–27

Material

Two reduncine crania with horn-cores from bed 3aN could belong to a smaller, more kob-like species of *Kobus*. They are L30391 and L31287, which are both frontlets with almost complete horn-cores and separate, almost complete crania (Figs 26–27). Their measurements are:

	L30391	L31287
Anteroposterior diameter at base of horn-core	43,8	37,6
Lateromedial diameter at base of horn-core	39,7	30,1
Minimum width across lateral sides of horn pedicels	89,1	88,6
Width across lateral edges of supraorbital foramina	c. 45,0	52,1
Occipital height from dorsal edge of foramen magnum	37,6	37,8
Skull width across mastoids behind external auditory meatus	93,3	94,0
Width across anterior tuberosities of basioccipital	22,9	28,6
Width across posterior tuberosities of basioccipital	27,0	35,0

Description

The horn-cores of L30391 differ from those of *Kobus subdolus* by being



Fig. 26. *Kobus* sp. 2. L30391, anterodorsal view of frontlet. Scale = 25 mm.

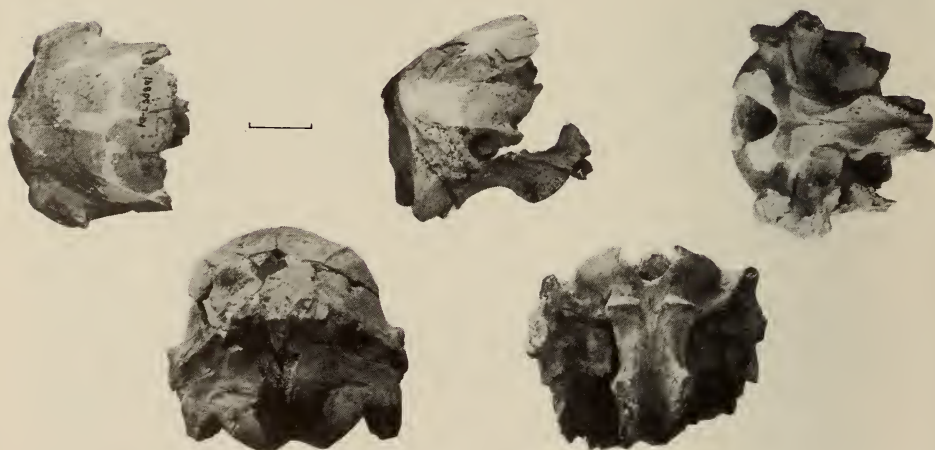


Fig. 27. *Kobus* sp. 2. Top row from the left: L30391, cranium in dorsal, lateral and ventral views. Bottom row: L31287, cranium in occipital and ventral views. Scale = 25 mm.

smaller, less squat and short, more divergent, and with stronger backward curvature at the base. The second specimen is also small and has not very squat horn-cores, but may have been too ontogenetically young to have acquired a basal backward curvature. Its horn-cores are also less divergent than in L30391, which would fit its supposed youthful age, but they are already more divergent than those of *Kobus subdolus*. It has no transverse ridges, unlike L30391. The division of specimens between this 'species' and the larger *Kobus subdolus* is not invariably clear cut. Two left and right horn-cores, L40870 and L40872, also from bed 3aN, look as if they could have come from one individual and have both been assigned to *Kobus subdolus*; however, they are strongly divergent and have more basal backward curvature than normal in that species.

The two crania differ from the cranium L2604, believed to go with *Kobus subdolus*, by the top of the braincase being convex instead of straight in profile and by a more emphasized dorsal rim on the mastoid. Less certain but possible differences are that the occipital surface may be relatively lower, the mastoid may be more restricted to the occipital surface, and the posterior tuberosities of the basioccipital are ridges directed laterally rather than posterolaterally.

An interesting character is that the central area of the frontals anteromedial to the supraorbital pits is more nearly horizontal and less slanted than in extant reduncines. It suggests that in complete specimens the conformation of the face as a whole would have been somewhat like that of modern deer or tragelaphines. Presumably such a state would be primitive for reduncines.

One expects a small *Kobus* to be kob-like, and it is interesting to compare this Langebaanweg form with some horn-cores L1-24, L1-25, frontlet L1-189, and a cranium, L1-291, from member B of the Shungura Formation which appear to belong to the kob ancestry. Unfortunately ancient damage has removed a number of key features of L1-291 such as the anterior tuberosities of the basioccipital, part of the nuchal crests and the median vertical occipital ridge. However, the Langebaanweg form can be seen to have horn-cores which show a closer approach to a posterolateral keel and hence are less rounded in cross-section posteromedially. It also has a transversely narrower occipital surface, a less rounded occipital edge, a narrower mastoid, and auditory bullae which are perhaps larger. However, in general the morphological agreement is good, and were it not for the problem of the teeth the east African and South African fossils could be taken as members of the same lineage at different time periods. The Langebaanweg horn-cores are those of a small *Kobus* with flattened lateral surface and an approach to a posterior keel and not at all like *Redunca*. In three of the characters by which they differ from *Kobus subdolus*, they resemble the Omo form: the profile of the braincase roof is slightly convex longitudinally, the mastoid is mainly confined to the occipital surface, and there is at least a slight development of the dorsal rim on the mastoid.

The two Langebaanweg crania may also be compared with BM(NH) M 35389, a cast of the holotype cranium, B798, of *Kobikeryx atavus* Pilgrim (1939: 125, fig. 14). Pilgrim took this as reduncine and supposed it was from

the Nagri or Dhok Pathan stages of the Siwaliks succession. The Langebaanweg fossils are larger and relatively wider across the occipital surface, but share with the Siwaliks fossil a slightly inclined and anteroposteriorly convex cranial roof and temporal lines which approach closely posteriorly and are not very prominent. The anterior tuberosities of the basioccipital take the form of distinctive longitudinal crests in both the Siwaliks fossil and L30391. The Siwaliks fossil has a moderately sized and inflated auditory bulla, but the state of this character is unknown in *Kobus* sp. 2. It is possible that B798 belongs to *Kobus porrecticornis*, already mentioned in the discussion of reduncine teeth and to be mentioned again in the account of Baard's Quarry fossils. If this were so, its non-boselaphine characters (inclined braincase roof, poorly developed temporal lines) would align it with the 'E' Quarry reduncine fossils in throwing doubt on the close relationship or descent of reduncines from boselaphines.

Tribe Alcelaphini

There are two similar sized species of Alcelaphini at Langebaanweg. There is no doubt of their tribal affinity on account of a suite of characters including frontals set at a high level between the horn-core bases in comparison with the dorsal parts of the orbital rims, extensive internal hollowing of the frontals and a single large smooth-walled sinus extending into the horn-core pedicel, the shallow and narrow postcornual fossa, small supraorbital pits, occipital surface facing laterally as well as backward and having a median vertical ridge and flanking hollows dorsally, basioccipital with a central longitudinal groove having its sides formed by ridges behind the anterior tuberosities, hypsodont cheek teeth, basal pillars on the teeth small or absent, and short premolar rows often accompanied by reduction and disappearance of P_2 s.

A nearly complete skull belonging to one of the species allows assessment of its facial characters and they, too, are clearly alcelaphine as appears from its diagnosis. For both species there are associations between horn-cores and teeth and in some cases postcranial bones as well, but it was found impossible to allocate teeth or postcranial bones at species level. There is no doubt of the marked primitiveness of the teeth, and this is one of the most interesting characteristics of these alcelaphines.

Damalacra gen. nov.

Type species

Damalacra neanica sp. nov.

Generic diagnosis

Moderate sized alcelaphines, a little smaller than the living *Alcelaphus buselaphus* or *Damaliscus lunatus*. Skull rather narrow as in those species and not wide as in *Connochaetes*. Horn-cores moderately long and without keels or transverse ridges. Horn-cores inserted fairly uprightly and close together. Shallow, elongated postcornual fossa. Frontals set at a high level between the horn bases in comparison with the dorsal parts of the orbital rims, orbital

rims project quite strongly, little or no central indentation of the parietofrontals suture, temporal lines on cranial roof do not approach closely posteriorly, braincase sides parallel, small supraorbital pits set close together. Occipital surface is wide and low and has a median vertical ridge, the mastoid has a large exposed area and is entirely contained within the occipital surface, the basioccipital is only slightly narrowed anteriorly if at all, it has anterior tuberosities of moderate size and a central longitudinal groove, the basisphenoid rises fairly sharply in front of the basioccipital, and the auditory bullae are moderate to large sized.

Hypsodont cheek teeth with not very rugose enamel, small basal pillars on M_1 s and dP_4 s and occasionally on upper molars, central cavities of upper molars not very complicated in outline, upper molars with rather strong styles but poor development of ribs between them, medial lobes of upper molars less well rounded than in Pleistocene and Recent alcelaphines, medial walls of lower molars with less pronounced outbowings and with more prominent metastylids than in later alcelaphines, lower molars without goat folds, central cavities of lower molars with hardly any transverse constrictions centrally, P_3 s reduced and often absent in life. P_4 s with posterior part of tooth (behind level of metaconid) less reduced than in later alcelaphines, generally with transverse orientation of the valley between entoconid and entostylid, and with paraconid and metaconid growing towards one another but not usually fusing.

The tibia has only a shallow posterior indentation in its distal articular facet, the metatarsal has a strong anterior longitudinal groove, otherwise the limb bones agree with those of later small or medium sized alcelaphines.

Etymology

The generic name comes from the Greek *damalis*, young cow or heifer, and *acra*, a cape.

Damalacra neanica sp. nov.

Figs 28–30, 34, 37

Holotype

L7257—a complete skull with horn-cores and upper dentitions comprising P^3 – M^3 on the right and a broken M^1 – M^3 on the left (Figs 28–29, 37).

Referred material

From bed 3aS:

L2573—cranium with horn-cores broken at their bases

L2680—cranium with the lower part of the left horn-core and base of the right

L12694A—cranium with most of the right horn-core and the lower part of the left; right maxilla with P^4 – M^3 (Fig. 30)

L40072—cranium with left horn-core

L40083—frontlet with basal half of horn-cores

L40154—cranium with basal half of right horn-core



Fig. 28. *Damalacra neanica*. L7257, holotype. Dorsal and ventral views. Scale = 50 mm.

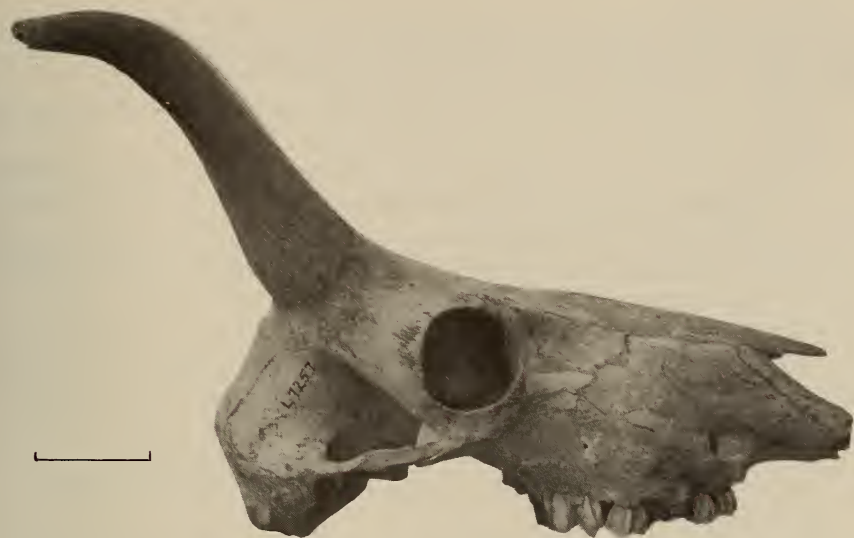


Fig. 29. *Damalacra neanica*. L7257, holotype. Lateral view.
Scale = 50 mm.

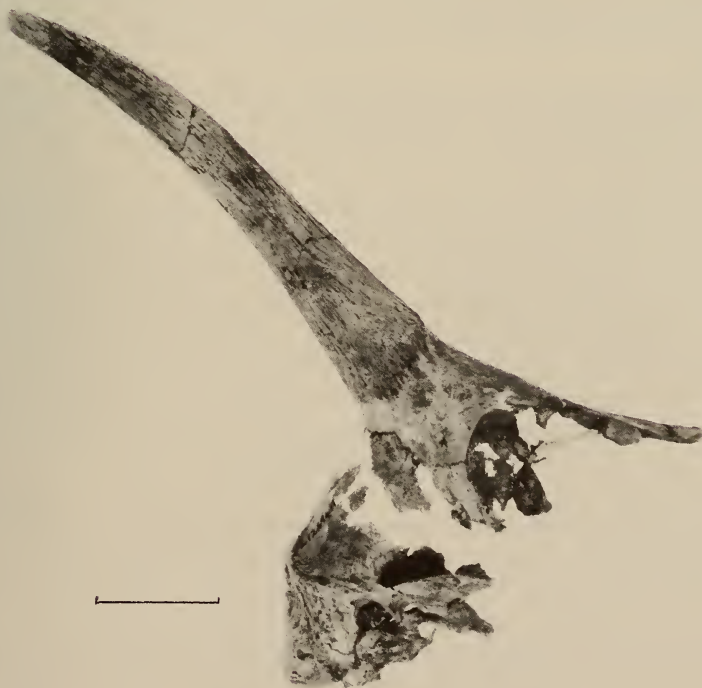


Fig. 30. *Damalacra neanica*. L12694A, cranium with horn-cores
in lateral view. Scale = 50 mm.

- L40166—left horn-core with midfrontal suture (Fig. 34)
 L40275—female frontlet with both horn-cores, possibly of this species
 L40537—left and right horn-cores, back of skull, skull fragments
 L41329—left horn-core and base of the right one from one individual
 L41710—left horn-core with mid-frontal suture
 L2608, L2614, L4617, L4618, L6590, L6595, L15720, L40054, L40055,
 L40168, L40173, L40514, L40752, L40754, L40756, L41019, L2619
 (immature)—left horn-cores
 L2607, L2613 (Fig. 37), L2668, L2670, L15015, L15809, L40110A, L40750
 —right horn-cores
 L6582A—horn-core of indeterminate side
 L40126A—left horn-core, a female, possibly of this species

From bed 3aN:

- L41414, L45085—left horn-cores
 Of uncertain origin (picked up by mine workers):
 L40761—cranium preserved from behind the level of the horn-cores
 L41330—back of cranium
 Dental and postcranial remains will be considered under the next species.

Horizon

The holotype and nearly all the other material of *Damalacra neanica* comes from bed 3aS of the PPM. No remains are known from the QSM.

Etymology

The specific name comes from the Greek *neanicos*, youthful, and refers to the place of this species early in the history of Alcelaphini.

Diagnosis

A species of *Damalacra* in which the horn-cores are without compression or slightly compressed anteroposteriorly, have no flattened lateral surface, taper fairly sharply from base to tip, show much increased divergence distally, have either slight backward or slight forward curvature in profile, and are inserted behind or above the back of the orbits. They have no very apparent torsion but it would have been anti-clockwise on the right side. The boundary between the pedicel top and the base of the horn-core is higher on the medial than on the lateral side of the horn-cores. It is probable that female horn-cores are smaller than those of males as in extant alcelaphines.

Frontals set at a notably high level between the horn bases in comparison with the dorsal part of the orbital rims, braincase roof strongly angled on face, straight in profile, and without a parietal boss. Nasals transversely domed, without lateral flanges anteriorly, wider relative to their length than in living *Alcelaphus* and *Damaliscus*, preorbital fossae moderately large and deep and with an upper rim, ethmoidal fissure absent, zygomatic arch somewhat deepened in its anterior parts, infraorbital foramen set high above the back of P³, premaxillae contacting the nasals and narrowing only slightly as they rise, median indentation at back of palate passing further anteriorly than the lateral ones,

cheek tooth-row less anteriorly positioned than in living *Alcelaphus* and *Damaliscus lunatus*, palatine foramina wide apart. The large mastoid exposure is especially expanded in its medioventral part, and the moderate to large auditory bullae are little inflated.

Remarks

The holotype skull is well preserved and lacks only the anterior parts of the premaxillae. The posteroventral surfaces of the skull around the basioccipital have been worn smooth by water rolling (Hendey 1970, fig. 3). The paired right and left mandibles, L7257C and D, were once thought to have come from the same individual as the skull, but their wear states are too early. However, it is possible, although not definite, that another right mandible, L7257B with teeth in a later state of wear, is from the same individual as the holotype.

The holotype and L12694A are specimens in which there is an association between horn-cores and teeth.

The cranium L40761 has the largest mastoid exposure seen in any *Damalacra* of either species, and it has also preserved its auditory bulla.

1 cranium, 3 frontlets and 33 horn-cores in the collection of *Damalacra* were taken as females. Of these, only the left horn-core L40126A and the frontlet L40275 are thought to be possibly of *D. neanica*. The insertion of their horn-cores is such that the longest cross-sectional diameter does not lie more or less parallel to the longitudinal midline of the skull. The remaining pieces will be considered under the next species.

The combination of a suite of specialized characters with a number of primitive characters is notable in this species. Among its primitive characters are the transversely straight parietofrontals suture, supraorbital pits set closely together, the large preorbital fossa, the nasals not very long or narrow, the tooth-row not positioned very anteriorly, and most of the tooth characters mentioned in the diagnosis. Against this one sees the specializations of horn-cores compressed anteroposteriorly if at all, without much backward curvature but with some distal divergence, inserted behind the orbits, the frontals well raised between the horn-core bases, and the shortness and steep inclination of the braincase roof. The shortness and steepness of the braincase roof must be a consequence of the short posterior migration of the horn-core bases, and one can appreciate that all the specialized characters are a simple unified set of changes.

The cranium L12694A is interesting as having the most primitive aspect of any specimen of this species. Its horn-cores are less anteroposteriorly compressed, their distal divergence is less, they still show appreciable backward curvature, and the braincase roof is longer.

A cranium, L40761, preserved forward to just behind the horn-cores, has a very large mastoid with the greatest expansion lying in the medioventral part of the bone. This matches *D. neanica* crania in which the mastoids are more expanded medioventrally than in *D. acalla*. Of six specimens of *D. neanica*,

only one, L40072, has mastoids apparently both small and not expanded medio-ventrally. Hence L40761 may be assigned to *D. neanica*, and it has the largest mastoid known in that species. The top of the braincase is less smooth in profile in L40761 than in other *D. neanica*, but straight enough to fit this species. The anterior tuberosities of its basioccipital are fairly narrow and this, too, may fit *D. neanica* better than *D. acalla*. L40761 has an auditory bulla and becomes the only specimen of *D. neanica* with this structure preserved. It is moderately large but not very inflated, and thereby differs from that of *D. acalla*, as seen in L40474, which is only slightly larger but much more inflated.

Measurements

Measurements on L7257 other than those shown in Table 4 are as follows. Length of nasals 133, breadth of nasals 32,8, length of frontals 128, minimum width of palate between medial borders of M²s 55,2. Both L7257 and L12694A had upper tooth rows with the following respective measurements: occlusal lengths M¹-M³ 61,5, 55,4; occlusal lengths M² 23,2, 21,0; occlusal lengths P⁴ 11,9, 11,7.

Measurements on the horn-cores and frontlets of *D. neanica* from bed 3aS, including specimens shown in Table 4, are:

	Number measured	Mean	Range	Standard deviation	Standard error
Anteroposterior diameter at base of horn-core, left side	17	40,8	35,6-45,2	3,1	0,75
Mediolateral diameter at base of horn-core, left side	17	41,5	36,2-51,3	4,6	0,99
Horn-core length	4	218	199-232	14,3	7,1
Minimum width across lateral sides of horn pedicels	6	99,9	95,8-107,3	4,7	1,92
Width across lateral edges of supra-orbital foramina	4	49,3	44,4-55,3	4,5	2,27

The female horn-core L40126A has an index $33,3 \times 28,8$.

Horn-core indices for L41414 and L45085 from bed 3aN are $43,3 \times 433$, and $39,8 \times 44,5$ respectively.

Comparisons

The only extant genus of alcelaphine which might be thought to resemble *Damalacra neanica* is *Beatragus*. The single living species, *B. hunteri*, had become restricted to a very small area of northern Kenya by the time of its discovery by Europeans in the last century (Ansell 1971). *B. antiquus* L. S. B. Leakey, 1965, is a larger extinct species known from Beds I and II at Olduvai Gorge and from uppermost member G of the Shungura Formation, Omo.

TABLE 4
Skull measurements of *Damalacra neanica*.

	L7257	L2573	L2680	L12694	L40072	L40083	L40154	L40537	L40761	L41330	L40275 female
Horn-core length	225	—	—	232	—	—	—	216	—	—	—
Anteroposterior diameter at base of horn-core	45,2	—	38,1	42,7	37,7	35,6	39,1	45,2	—	—	32,2
Mediolateral diameter at base of horn-core	44,0	—	36,7	36,2	40,6	36,9	38,0	—	—	—	29,0
Minimum width across lateral surfaces of horn pedicels	107,3	—	95,8	97,5	103,9	99,0	—	—	—	—	82,3
Width across lateral edges of supraorbital pits	49,4	—	—	—	55,3	44,4	47,9	—	—	—	50,4
Length of skull top from occipital top to back of frontals	53,5	—	53,4	63,0	47,1	—	48,3	—	50,9	—	—
Maximum braincase width	82,4	74,4	79,2	82,6	80,2	—	74,1	—	77,9	—	—
Skull width across mastoids behind external auditory meati	109,5	—	100,0	107,0	—	—	102,6	110,2	118,0	109,4	—
Occipital height from top of foramen magnum	—	c. 33,0	36,3	33,6	—	—	35,0	35,3	41,8	42,3	—
Width across anterior tuberosities of basi-occipital	—	—	26,6	27,0	—	—	25,1	31,4	27,0	29,4	—
Width across posterior tuberosities of basi-occipital	—	33,3	34,5	33,2	—	—	36,7	37,6	38,5	39,3	—

The anteroposterior compression of so many of the horn-cores of *Damalacra neanica* causes them to resemble the horn-cores of *B. antiquus* and, less closely, the larger horned males of *B. hunteri*. The torsion of *D. neanica* horn-cores, in so far as it exists at all, is anti-clockwise on the right side, and this, too, is a resemblance to *Beatragus*. However, the Langebaanweg alcelaphine is too primitive to be satisfactorily related to *Beatragus*. It is difficult to visualize two horn-core characters being held relatively steady over several million years while all other skull characters underwent evolutionary advance. Further comparisons with other alcelaphines will be made in the discussion of *Damalacra acalla*.

Damalacra acalla sp. nov.

Figs 31–35, 37–38, 40

Hippotragini sp. Gentry in Hende, 1970: 115.

Holotype

L40001—a cranium with much of the right and the lower part of the left horn-core (Fig. 31).

Referred material

The major specimens assigned to this species are as follows:

From bed 3aS:

L1799—frontlet with skull fragments

L1836—frontlet with some isolated, partly fragmented left and right upper teeth, skull fragments, vertebrae (Hende 1970, pl. 4, fig. C). (Figs 32, 37)

L12427—frontlet with horn-core bases, occipital surface, braincase roof, basioccipital, two atlas vertebrae and a crushed palate with P²—broken M³

L20187—frontlet with both horn-cores, back of skull with basioccipital

L40096—cranium with horn-core bases (Fig. 35)

L40225—female cranium with both horn-cores (Fig. 38)

L40319—frontlet with complete horn-cores, right and left maxillae with P³—M³, metatarsal, atlas and axis

L40474—cranium with parts of both horn-cores

L41832—frontlet with horn-cores, vertebrae

L2615, L15928, L40288, L40493—frontlets

L2616 (Figs 34, 37), L2622, L2624, L2625, L2632, L2649, L3587, L16280, L40025, L40120A, L40155A, L40163, L40165, L40167, L40171, L40172, L40178, L40278, L40723, L41327, L41368—left horn-cores
L2622, L2623, L2628, L2629, L2633, L2638, L2665, L3489, L6592, L40048, L40050, L40074, L40123A, L40161, L40177, L40187, L40248, L41092, L41202, L41706—right horn-cores

L10563—female left horn-core



Fig. 31. *Damalacra acalla*. L40001, holotype. Cranium in dorsal and lateral views.
Scale = 25 mm.

From QSM or bed 3aS:

L12856—damaged cranium with base of right horn-core

L22278—left horn-core, basioccipital, atlas, vertebral fragments, left maxilla with P^2 – M^3 and right mandible with P_4 – M_3 (no P_2 in life). (Fig. 39)

L24809—right horn-core, part of the left horn-core, basioccipital, skull fragments, three left upper molars, two right upper molars

From bed 3aN:

L46075—cranium with horn-cores

L33832, L41412, L46040 (Fig. 33)—frontlets

L46042, L46061, L46072—left horn-cores

L30215, L45012, L46039, L46043, L46047, L46061, L46068—right horn-cores

From beds 3aS or 3aN:

L40751, L40757—left horn-cores

L40758, L40793—right horn-cores.

L46072 and L40793 may belong to *Damalacra neanica*.

Associations between horn-cores and teeth are provided by L1836, L12427, L22278, L24809, and L40319.



Fig. 32. *Damalacra acalla*. L1836, frontlet in anterior view. Scale = 50 mm.



Fig. 33. *Damalacra acalla*. L46040, frontlet in anterior view. Scale = 25 mm.



Fig. 34. From the left: *Damalacra neanica* L40166, left horn-core in anterior and lateral views. *D. acalla* L2616, same views. Scale = 25 mm.



Fig. 35. *Damalacra acalla*. L40096, cranium in occipital and ventral views. Scale = 25 mm.

Horizon

The holotype comes from bed 3aS of the PPM. Most of the other material comes from 3aS, but this species is better represented in bed 3aN than is *D. neanica* and three fossils are possibly from the QSM. A left mandible, L12883, is from the QSM, but it cannot be ascertained to which species of *Damalacra* it belongs.

Diagnosis

An alcelaphine in which the cranial size and proportions are similar to *Damalacra neanica*. Horn-cores differ from those of *D. neanica* by being compressed in the mediolateral plane if at all, often with a localized, usually medial, swelling at their bases, sometimes tending to have a flattened lateral surface along part of their length, with more definite backward curvature and less marked distal divergence, inserted closer behind the orbits, and with a more nearly horizontal boundary between the top of the pedicel and the horn-core proper. Other differences from *D. neanica* are that the braincase roof is less steeply inclined, more curved in profile, and with an insignificant parietal hump which is about as well developed as in living *Damaliscus*; the mastoid exposure large but less expanded especially medioventrally, and the auditory bullae slightly larger and much more inflated.

Female horn-cores are smaller than those of the males as in extant alcelaphines. Tooth characters are taken not to differ from *D. neanica*.

Etymology

The specific name is from the Greek *acalles*, without charms, and refers to the primitive state of nearly all the characters in this species.

Remarks

No fossil has been preserved with a face, so no facial characters appear in the diagnosis. One cannot assume that the face would differ very much from

that of *Damalacra neanica*.

There can be little doubt that the two alcelaphine species are closely related. It is interesting that *D. acalla* has many characters which appear to be primitive just as in *D. neanica*, but hardly any which are specialized. Primitive characters are the transversely straight parietofrontals suture, the supraorbital pits not set wide apart, most of the characters of the horn-cores, the fairly long braincase and its not very inclined roof, and the characters of the cheek teeth. Figure 36 shows the difference in horn-core compression between *D. acalla* and *D. neanica*, and also that *D. neanica* has different cranial proportions in the form of a shorter braincase and a lower and wider occipital surface. The extant *Damaliscus dorcas*, shown on the same figure, has cranial proportions similar to *Damalacra acalla*, but rather small horn-cores and a relatively narrow width across the anterior tuberosities of the basioccipital. Figure 37 shows cross-sections of *Damalacra* horn-cores.

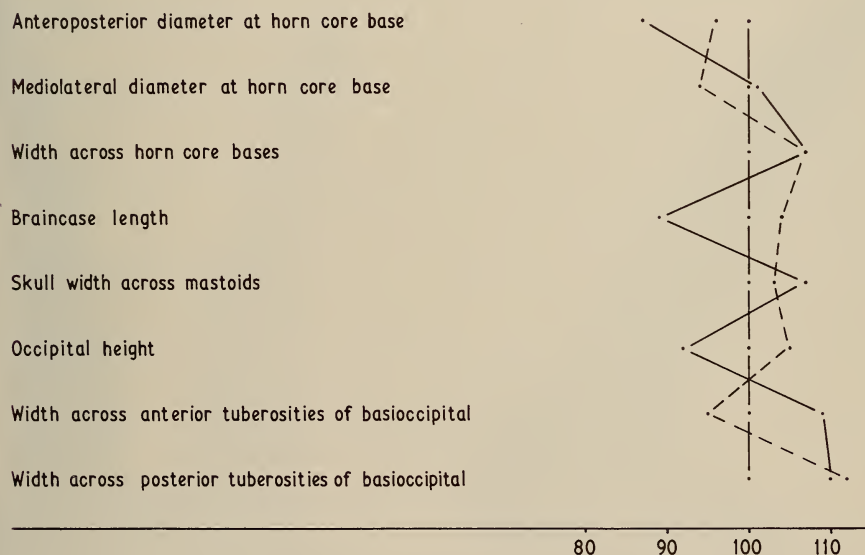


Fig. 36. Percentage diagram of skull measurements in Alcelaphini. The standard line at 100 per cent is for seven *Damalacra acalla* from bed 3aS. The other continuous line is for six *D. neanica* including L12694A, and the dashed line is for four male *Damaliscus dorcas*. Not all measurements were available on all the fossils.

Among the female remains of *Damalacra* only a horn-core and a frontlet, L40126A and L40275, are thought to be of *D. neanica*. Another two are thought to be definitely of *D. acalla*; these are the cranium L40225 and the left horn-core L10563. The remaining horn-cores appear to be attenuated versions of *D. acalla* male horn-cores, but one cannot be certain that the females of *D. neanica* might not have more primitive horn-cores than the males.

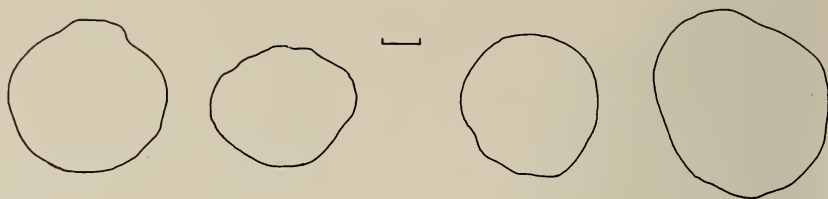


Fig. 37. Cross-sections of *Damalacra* horn-cores at a distance above the pedicel top equal to half the anteroposterior basal diameter. All are shown as if they were of the right side. Lateral sides are towards the left and anterior sides towards the base of the illustration. From the left: *D. neanica* L7257 (holotype) and L2613, *D. acalla* L1836 and L2616. Scale = 10 mm.



Fig. 38. *Damalacra acalla*. L40225, female cranium in lateral and anterior views. Scale = 25 mm.

L46075 is an alcelaphine cranium with horn-cores from bed 3aN, apparently belonging to *D. acalla*, but differing from those in bed 3aS by its horn-cores being slightly less compressed mediolaterally, the braincase roof shorter, and the anterior tuberosities of the basioccipital wide apart. Its most instructive comparison is with L12694A which has the most primitive aspect of any *D. neanica* cranium. L46075 is larger, its horn-cores differ little in their degree of compression, they diverge distally but less than in L12694A, they have a slight backward curvature but less than L12694A, their insertion is less upright in side view than in L12694A, the pedicel is not higher on the medial than the lateral side of the horn-core as in L12694A (and other *D. neanica*), the braincase roof has a slightly curved profile, whereas L12694A is straight, and the mastoid is not expanded medioventrally and is certainly less so than in L12694A. The anterior tuberosities of the basioccipital are much wider apart than in L12694A or any other examples of *D. neanica*. It is interesting that the relative lack of backward curvature of the horn-cores makes them more like *D. neanica* than are those of L12694A.

The total sample of horn-cores of *D. acalla* does not show that antero-posterior compression has increased in bed 3aN in comparison with 3aS, but a size increase has taken place (Fig. 39). The differences between the 3aS and 3aN samples of horn-cores for both anteroposterior and mediolateral diameters (measurements given below) are significant at the 5 per cent level. The values of *T* were 2,39 and 2,88 for 27 degrees of freedom, and confirm the size increase. Samples for the measurement of minimum width across the lateral sides of the horn-core pedicels were smaller but similarly showed a size increase from bed 3aS to 3aN. The value of *T* was 3,13 for 10 degrees of freedom which is significant at the 5 per cent level. Measurements also suggest that the horn-cores decreased in length from 3aS to 3aN but in this case the difference was not statistically significant. In general the *D. acalla* in bed 3aN looks more robustly built across the frontals and horn-core bases than in bed 3aS, and the frontals are more raised between the horn-core bases. As the horn-cores and their supporting pedicels become larger, so the projection of the dorsal part of the orbital rims becomes less obvious. On the paired horn-cores L46061, the localized basal swelling is confined to the middle part of the medial side and the top of the sinus in the pedicel comes level only with the junction of the pedicel top and horn-core proper. Their basal index is $55,3 \times 50,3$. Numbers of such horn-cores are coming to light in the material being processed from bed 3aN (Q. B. Hendey, pers. comm. 29 August 1978).

The characters of the teeth of *Damalacra* have been mentioned in the generic diagnosis and the teeth are illustrated in Figures 40–42. They are about the size of the teeth of *Damaliscus lunatus*, whereas the size of horn-cores, crania and postcranial bones of *Damalacra* is in closer agreement with *Damaliscus dorcas*, a species smaller than *D. lunatus*. Even the mandibular rami of *Damalacra* are only about as large as in *Damaliscus dorcas*. It was not found possible to differentiate between the two species of *Damalacra* on their teeth.

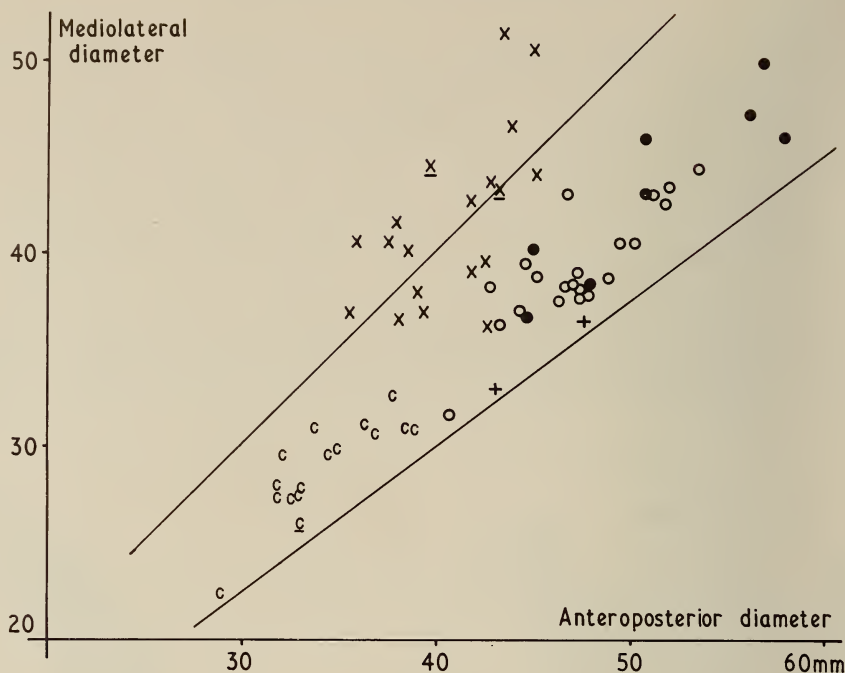


Fig. 39. Basal diameters of *Damalacra* horn-cores. X = *D. neanica* lefts from bed 3aS, X = the same from bed 3aN, O = *D. acalla* rights, the solid ones from bed 3aN and the rest from bed 3aS, + = *D. neanica* L22278 and L24809 from QSM, C = *Damalacra* female left horn-cores, the underlined one from bed 3aN and the rest from 3aS, Upper diagonal line = 100%, lower one = 75% as in Figure 3.

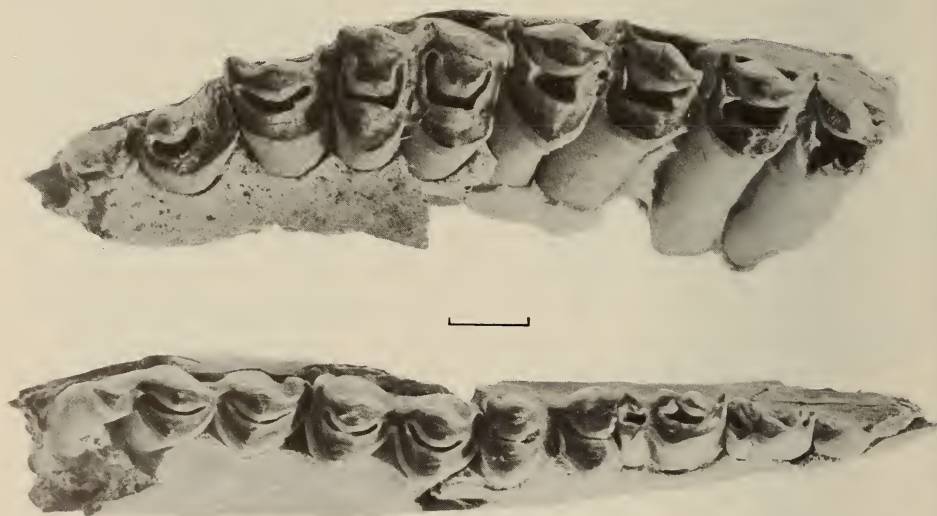


Fig. 40. *Damalacra acalla* L22278, occlusal view of left upper dentition. *Damalacra* sp. L40534, occlusal view of right lower dentition. Scale = 10 mm.



Fig. 41. *Damalacra* sp. L41482, lateral view of left mandible.
Scale = 50 mm.

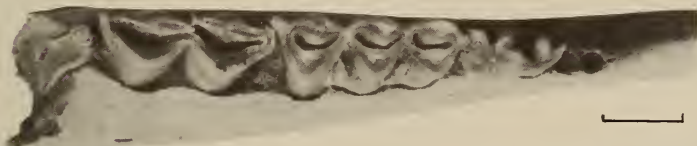
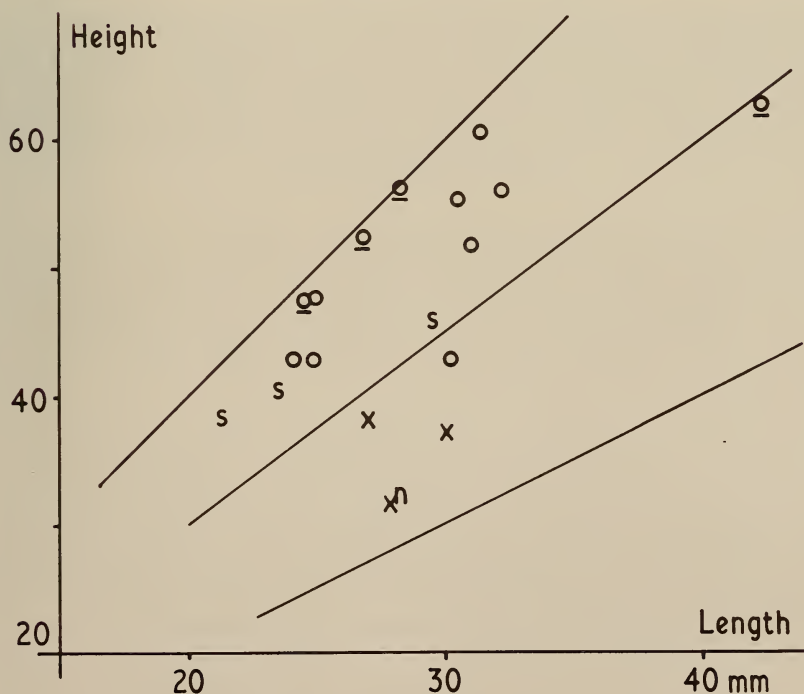


Fig. 42. *Damalacra* sp. L11612, occlusal view of immature right lower dentition with dP_3 - M_1 , alveoli for dP_2 and a fragment of M_2 .
Scale = 10 mm.



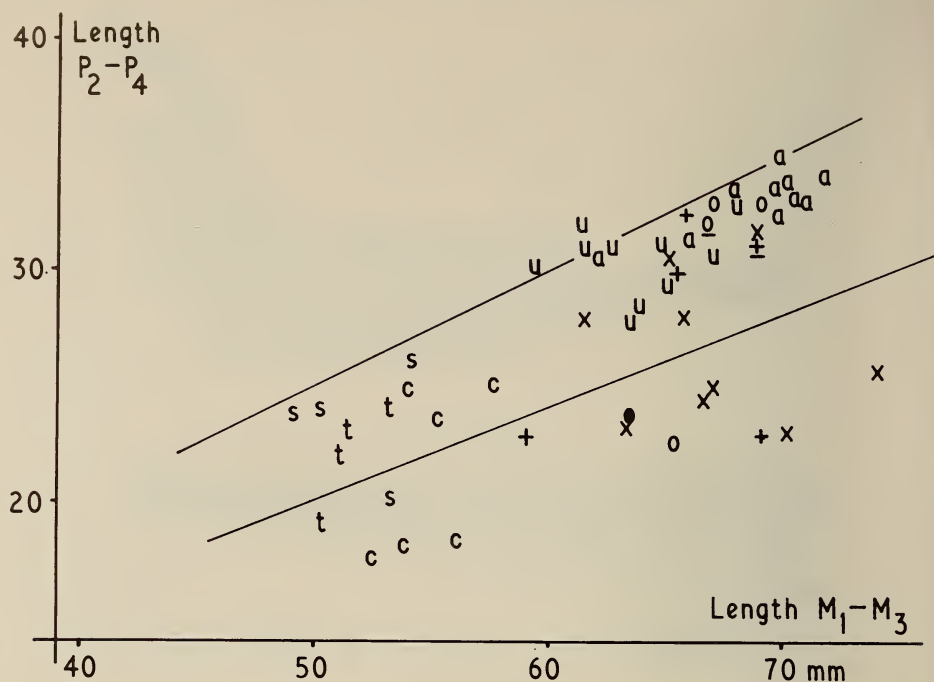


Fig. 44. Occlusal lengths of lower premolar and molar rows in Alcelaphini and in bovids from Fort Ternan. X = *Damalacra* rights, O = lefts, + = both sides, underlined readings^s are bed 3aN, the rest are bed 3aS, solid circle is L12883 from QSM. a = extant *Alcelaphus buselaphus*, c = extant *Damaliscus dorcas*, u = extant *D. lunatus*, s = ?*Pseudotragus potwaricus* from Fort Ternan, t = *Oioceros tanyceras* from Fort Ternan. Upper diagonal line = 50%, lower one = 40% as in Figure 3. The readings for all species below the 40 per cent line are those without P₂ in life.

The most interesting feature of the teeth is the primitive state of so many of their characters. Figure 43 shows how their hypsodonty is less than in extant and other fossil alcelaphines. In Langebaanweg times unworn M₃s were only about two-thirds as high crowned as in the Middle Pleistocene and later. The difference much exceeds that between Sterkfontein Type Site and the most recent sample.

It is interesting against this background that trends to the reduction and loss of P₂ were already present. Out of 36 specimens in which its presence or absence could be ascertained, 21 had it and 15 were without. Of the 21 with it only 4 were in later middle or late wear, while of the 15 without it 10 were in later middle or late wear. The trend to reduction and loss of P₂ may exist about as much as in *Parmularius altidens* of Bed I, Olduvai Gorge, in which three out of eight specimens lacked it, and is certainly in advance of modern *Damaliscus lunatus* and *Alcelaphus* in which P₂ is practically always present. However, *Parmularius* has reduced its whole premolar row more than in *Damalacra* (Fig. 44) and hence P₄ is smaller relative to M₂ (Fig. 45).

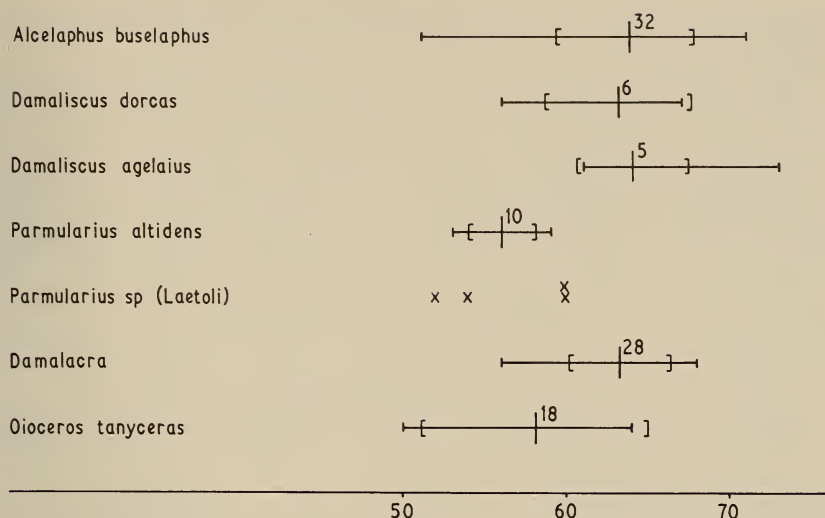


Fig. 45. Occlusal length of P_4 expressed as a percentage of that of M_2 in alcelaphines. For each species the range is shown by a horizontal line, mean value by a short vertical line, standard deviation by squared brackets, and the number of specimens by the figure adjacent to the mean.

The Langebaanweg alcelaphine teeth are the earliest known which are definitely of this tribe, and they make an interesting comparison with those of the much earlier Caprini, *Oioceros tanyceras* and *Pseudotragus? potwaricus* which are candidates for alcelaphine ancestry (and might eventually have to be transferred to that tribe to preserve monophyly). These forms are from Fort Ternan and Ngorora (Gentry 1970a, 1978a). The Langebaanweg teeth are larger, more hypsodont than the *Oioceros* if not also than the *Pseudotragus?*, the basal pillars are much less evident, the paraconid and metaconid of P_4 are either growing toward one another or fused, the entoconid and entoconulid remain separate on P_4 later in wear, the medial wall of the back lobe of M_3 is perhaps more clearly offset laterally in earlier wear, and the central cavities of the lower molars show less sign of being transversely constricted centrally. The first four of these characters are more advanced at Langebaanweg, the next two may be linked with larger size and the last appears to be more primitive. Some characters are unchanged: the degree of rounding of the walls of the medial and lateral lobes on the lower molars, the shape of the medial lobes of the upper molars, and the level of development of styles on the upper molars. Some examples of both Fort Ternan species are already without P_2 s in life (Gentry 1970a: 265, 285) but this trend has been taken further at Langebaanweg. Moreover, there is less tendency to reduction of P_2 at Fort Ternan, as can be seen in Figure 45 where the relatively small size of P_4 is a consequence of the relatively unreduced P_2 . Overall the Fort Ternan premolar rows are as long as at Langebaanweg (Fig. 44). Some of the morphological differences between Langebaan-

weg alcelaphine teeth, those of other alcelaphines and the Fort Ternan caprines are shown in Figure 46.

Alcelaphine postcranial bones from 'E' Quarry are of appropriate size to be conspecific with the cranial and dental remains of the *Damalacra* species. The following notes are based on an associated skeleton, L41482 (Figs 21, 47–48), from bed 3aS with complete examples of all the long limb bones, as well as on other examples. The lengths and least transverse thicknesses of the long limb bones of L41482 are as follows: femur $224 \times 22,2$, tibia $269 \times 22,7$, metatarsal $223 \times 16,9$, humerus $195 \times 20,4$, radius $226 \times c. 23,6$, metacarpal $201 \times 17,9$.

Chief among the other limb bones are the following:

From bed 3aS:

L12456—much of right humerus, proximal and distal right radius

L12463—distal right tibia, associated with above

L15000—complete right metacarpal with length and least transverse thickness of $226 \times 19,1$

L15031—right scapula

L15075, L15155—complete left and right humeri with lengths and least transverse thicknesses of $197 \times 22,0$ and $176 \times 19,3$

L15271—most of right humerus

L15276—distal metatarsal

L15963—distal right humerus

L40279—complete left metacarpal with length and least transverse thickness of $199 \times 17,3$

L40319—complete metatarsal with length and least transverse thickness of $224 \times 17,9$, atlas vertebra

L41216—distal left humerus, distal left radius, proximal left metacarpal, left and right proximal metatarsals

Probably from bed 3aS:

L1848, L3037—distal left and distal right femora

L2189, L3042—complete left and right metatarsals with lengths and least transverse thicknesses of $220 \times 16,8$ and $228 \times 17,4$

L2167, L12280—distal right and distal left tibiae

From bed 3aN:

L30769—distal left humerus, distal right radius; probably alcelaphine

L31388—distal right humerus

L31684—distal right tibia and proximal right metatarsal

L32707—distal left tibia and complete left metatarsal with length and least transverse thickness of $c. 237 \times c. 18,6$

Generally the Langebaanweg bones show the typical characters of alcelaphines, most of which are cursorial adaptations (Gentry 1970a: 277–282), but often less sharply defined than in extant species. The metapodials may be thicker than in the similarly sized *Damaliscus dorcas* and are about as thick as in later, larger alcelaphines (Fig. 49). The metacarpals are not as long relative

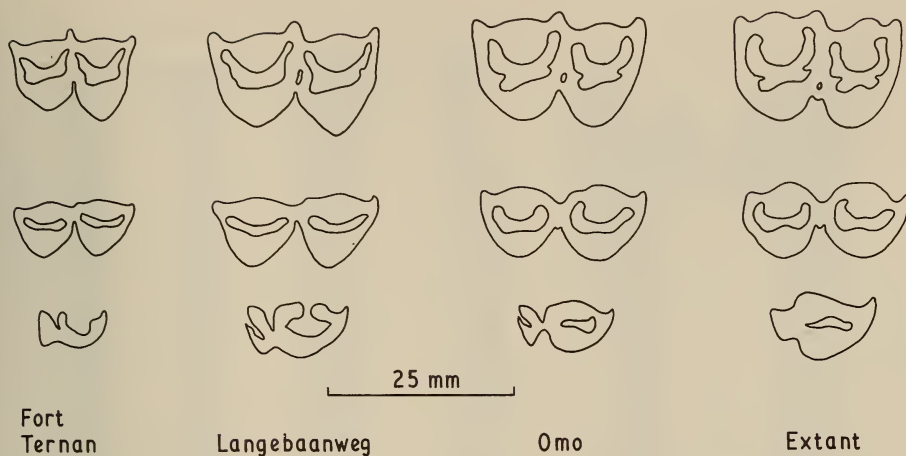


Fig. 46. Occlusal views of M^2 (top row), M_2 (middle row) and P_4 (bottom row) of Caprini from Fort Ternan, *Damalacra* from E Quarry Langebaanweg, Alcelaphini from the Shungura Formation Omo, and extant *Alcelaphus buselaphus*. All teeth are of the right side and the anterior direction lies to the right.



Fig. 47. *Damalacra* sp. L41482, long limb bones of hind leg. From the left: right femur in lateral and anterior view, left tibia in medial and anterior view, right metatarsal in lateral and anterior views. Scale = 25 mm.



Fig. 48. *Damalacra* sp. L41482, long limb bones of foreleg. From the left: left humerus in lateral and anterior view, right radius in medial and anterior view, left metacarpal in posterior and anterior view. Scale = 25 mm.

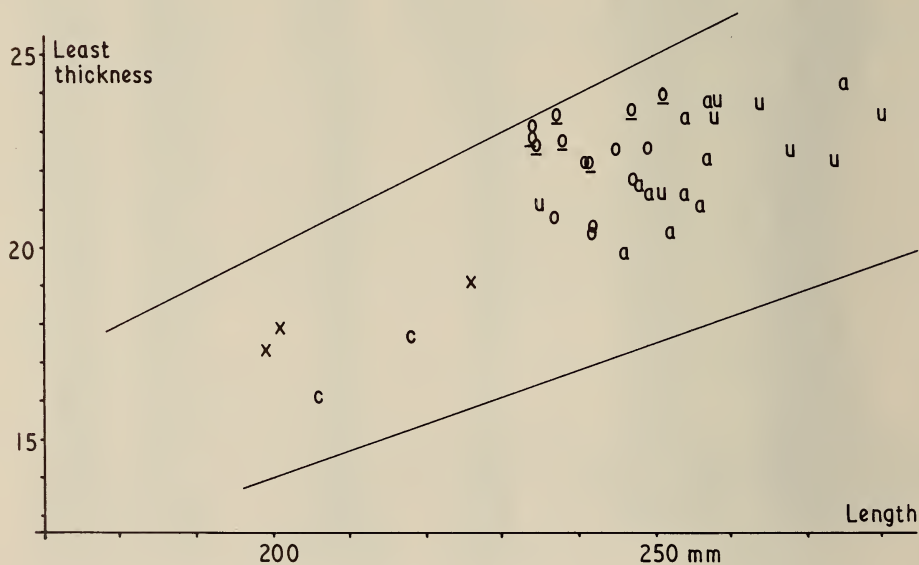


Fig. 49. Proportions of alcelaphine metacarpals. X = bed 3aS, E Quarry Langebaanweg. a = extant *Alcelaphus buselaphus*, c = extant *Damaliscus dorcas*, u = extant *D. lunatus*, o = *Parmularius altidens*, rights underlined. Upper diagonal line = 10%, lower one = 7% as in Figure 3.

to the metatarsals as in extant *Damaliscus lunatus* or *Alcelaphus buselaphus*. The only characters in which they are definitely different or less advanced have been mentioned in the generic diagnosis. The femur shows an anteroposteriorly long lateral part of the articular head, a deep hollow between the articular head and the great trochanter, well-marked insertion positions for muscles and ligaments on the distal lateral condyle, and a medial condyle which projects well anteriorly. However, it is possible that the patellar fossa distally is less extremely wide and the lateral roughened fossa less deep than in living alcelaphines. The tibia shows a strong central swelling on the top articular surface and a depression medial to it just in front of the level of the paired flanges, themselves well marked. There is an upcurved edge of the lateral facet at the proximal end, and the medialmost muscle scar at the top of the posterior surface is long, strong, high on the shaft and in a relatively medial position. Distally the medial malleolus is not clearly shorter than in living alcelaphines, and the front fibula facet is well outlined and distinct from the rear one. The presence of a patellar groove at the front of the proximal articular surface is like *Connochaetes* rather than *Alcelaphus* and *Damaliscus*. The back edge of the distal articular facets is less indented centrally than in most extant alcelaphines in L2167, L41482 and L32707, but L31684 does not appear to be different. The metatarsal has the posterior part of its top articular surface transversely narrower than the central parts, a small main facet for the naviculocuboid, no deep hollow between the anterior and posterior naviculocuboid facets, parallel outer edges of the distal condyles, deep hollows above the distal condyles anteriorly, and strong paired flanges distally on the anterior surface. The ridges on the condyles pass high posteriorly. However, the posteromedial part of the main naviculocuboid facet may have been more strongly raised than in living alcelaphines, the hollow deeper around the foramen at the top of the posterior surface (a character as in *Connochaetes*), and the distal condyles frequently have the appearance of being less high and narrow overall. The single complete metatarsal from bed 3aN is larger than examples from 3aS.

In the scapula the tuber scapulae is situated near to the lateral side in ventral view, the area for the origin of the teres minor muscle is well hollowed, and there is a slight flattening of the posterolateral edge of the glenoid facet. In the humerus the bicipital groove is wide and set back from the front edge of the lateral tuberosity, and a sharp ridge down the front of the tuberosity is variably developed. The distal end is completely alcelaphine with upright condyles of the articular surface, a strong medial groove, an indentation in the top of the medial condyle and a V-shaped prolongation of the lateral surface. However, the last character is not well marked in L15075, L31388A or L41482; it is better in L12456 and L41216. Two other possible differences from living alcelaphines are that the top of the medial tuberosity forms a less upstanding point and that the lateral tuberosity rises higher above the top of the infraspinatus scar in lateral view. In the radius the proximal lateral tubercle is large and set high, there is no rim on the medial side of the proximal medial facet,

the back of the lateral facet is set forwards, and distally the anterior flanges are strong and set close together. However, L41216 has rather a poor medioposterior hollowing for the scaphoid and L12456A is rather swollen distally in side view for an alcelaphine. The metacarpal of L41482 shows an angled anteromedial corner to its magnumtrapezoid facet as is usual in Alcelaphini but the unciform facet is perhaps larger. Another metacarpal, L15000, shows the converse conditions for these characters.

In the two atlas vertebrae, L40319 and L41482 (Fig. 50), the side edges are not concave over a very great length, and the front edge of the dorsal surface is not very indented. An alcelaphine character which both do show is a forwardly directed spike centrally at the front of the ventral surface.



Fig. 50. *Damalacra* sp. L41482. From the left: atlas vertebra in dorsal and ventral views, axis vertebra in left lateral view. Anterior sides towards the left. Scale = 25 mm.

Measurements

Measurements on three frontlets of *D. acalla* are:

	L1799	L1836	L15928
Skull width across posterior side of orbits	—	133,8	—
Length of horn-core along its front edge	—	265	—
Anteroposterior diameter at base of horn-core	45,2	42,9	44,4
Mediolateral diameter at base of horn-core	38,8	38,2	37,0
Minimum width across lateral sides of horn pedicels	90,3	90,3	94,3
Width across lateral edges of supra-orbital foramina	—	46,3	51,3

TABLE 5
Skull measurements of *Damalatra acalla*.

	L40001	L12427	L20187	L24809	L40096	L40474	L46075	L40225 female
Horn-core length	—	—	—	252	—	—	216	—
Anteroposterior diameter at base of horn-core	53,7	40,7	44,7	43,0	47,4	—	50,9	34,5
Mediolateral diameter at base of horn-core	44,3	31,7	39,4	33,0	39,0	—	45,8	29,7
Minimum width across lateral surfaces of horn pedicels	99,0	—	96,8	—	96,3	—	<103	78,6
Width across lateral edges of supraorbital pits	—	—	—	—	44,1	—	—	—
Length of skull top from occipital top to back of frontals	63,9	—	—	—	63,2	51,8	54,8	60,4
Maximum braincase width	c. 76,5	—	—	—	75,6	82,7	80,0	—
Skull width across mastoids behind external auditory meati	100,0	—	c. 95,0	—	94,4	106,5	114,7	—
Occipital height from top of foramen magnum	40,2	36,6	36,3	—	41,4	36,3	43,3	—
Width across anterior tuberosities of basioccipital	23,5	—	21,6	23,4	26,6	29,2	32,6	—
Width across posterior tuberosities of basioccipital	30,8	32,8	32,4	32,2	30,9	35,2	30,5	—

The widths across the anterior and posterior tuberosities of the basi-occipital of L12856 are 26,9 and 30,9. Additional measurements on L12427, not shown in Table 5, are occlusal lengths of M² 24,8, of P²-P⁴ 39,4, of P² 10,9, of P⁴ 12,2. The female horn-core L10563 has an index of 32,9 × 27,4.

Measurements on horn-cores and frontlets of *D. acalla*, including specimens listed in Table 5, are:

	Number measured	Mean	Range	Standard deviation	Standard error
Anteroposterior diameter at base of horn-core, bed 3aS, right side .	21	47,5	40,7-53,7	3,3	0,72
Mediolateral diameter of above . .	21	39,3	31,7-44,3	2,9	0,63
Anteroposterior diameter at base of horn-core, bed 3aN, right side .	8	51,4	44,7-58,2	5,3	1,89
Mediolateral diameter of above . .	8	43,4	36,7-49,9	4,6	1,63
Horn-core length, bed 3aS . .	4	240	216-265	21,6	10,8
Minimum width across lateral sides of horn pedicels, bed 3aS	9	96,4	90,3-101,7	4,1	1,35
Width across lateral edges of supra-orbital foramina, bed 3aS . .	5	49,3	44,1-54,2	4,1	1,81

Readings on the female horn-cores of *Damalacra* from bed 3aS, apart from the four assigned to species, are:

	Number measured	Mean	Range	Standard deviation	Standard error
Anteroposterior diameter at base of horn-core . .	26	34,3	28,9-38,9	2,6	0,51
Mediolateral diameter at base of horn-core . . .	26	29,0	22,4-32,6	2,2	0,44
Individual readings for specimens from bed 3aN were:					
Horn-core lengths	213, 216				
Minimum width across lateral sides of horn pedicels				98,9, 107,9	111,9
Width across lateral edges of supraorbital foramina				55,7	

Readings for occlusal lengths of alcelaphine lower teeth in middle wear are:

	Number measured	Mean	Range	Standard deviation	Standard error	Coefficient of variation
M ₁ -M ₃ , bed 3aS, right . . .	21	66,7	59,2-74,3	3,4	0,75	5,10
M ₁ -M ₃ , bed 3aN, left . . .	5	65,9	60,6-68,9	3,1	1,40	4,70
M ₂ , bed 3aS, right	29	21,8	19,0-25,2	1,3	0,24	5,96
M ₂ , bed 3aN, left	5	22,1	20,0-23,3	1,3	0,58	5,88
M ₃ , bed 3aS, left .	49	28,8	25,7-32,3	1,7	0,24	5,90
M ₃ , bed 3aN, left	8	28,4	26,8-30,4	1,4	0,48	4,93
P ₂ -P ₄ (with P ₂), bed 3aS, right	11	28,0	21,3-33,3	3,9	1,17	13,9
P ₂ -P ₄ (without P ₂), bed 3aS, right	6	24,2	22,6-29,9	2,9	1,16	12,0
P ₂ -P ₄ (with P ₂), bed 3aN, left	2	31,6	31,2-32,0	—	—	—
P ₂ , bed 3aS, right .	8	6,8	5,8-7,8	0,6	0,23	8,8
P ₂ , bed 3aN, left .	2	7,2	6,9-7,5	—	—	—
P ₄ , bed 3aS, right .	40	13,9	12,6-15,9	0,7	0,11	5,04
P ₄ , bed 3aN, left .	5	14,0	12,8-15,0	0,9	0,40	6,43

The coefficients of variation show that measurements of the occlusal lengths of P₂-P₄ and P₂ are particularly variable. Either the reduction in size of P₂ or the difficulty of identifying measuring points at the front and back of the premolar row may have an effect here, but it is also possible that the large coefficient of variation shows that one of the two species of *Damalacra* has a shorter premolar row than the other one. There is no indication that tooth size increased from bed 3aS to 3aN, in contrast to the indication from horn-cores.

Comparisons

It is informative to compare both species of *Damalacra* with a number of alcelaphine specimens from the Hadar Formation, Afar, which may represent an early member of the group in which *Parmularius*, *Damaliscus* and *Alcelaphus* evolved. The conclusion reached will be that *Damalacra* represents a still more primitive stage of alcelaphine evolution and is of uncertain relationship to the

Afar remains. The main Afar remains are:

AL 208-7	largely complete skull	from SH-3 surface
AL 353-3	cranium with left horn-core	from SH-2 surface
AL 161-5	cranium with base of left horn-core	from DD-3 surface
AL 120-2	pair of horn-cores and parts of associated skeleton	from DD-3 surface
AL 310-18	cranium with base of right horn-core	

The Afar alcelaphine shows the following characters: size about equal to extant *Damaliscus lunatus* and *Alcelaphus*; horn-cores of short to moderate length, without much compression, without a flattened lateral surface, without keels or transverse ridges, base often squared off posteromedially, thickness of cross-section often diminishing rapidly above the base and producing a tapered appearance, inserted close together above the back of the orbits, little divergent basally but more so distally, boundaries between pedicel tops and horn-core bases higher on the medial than the lateral sides; postcornual fossa long and shallow, parietofrontals suture with little central indentation, frontals raised between horn-core bases, orbital rims not projecting as a separate structure from the descending lateral surface of the horn pedicels, braincase roof short and inclined, near absence of a *Parmularius*-like parietal boss, braincase widening posteriorly, a deep face, long and narrow nasals, a large and fairly deep preorbital fossa, occipital surface with a strong median vertical ridge, and ventral border of the mastoid angled instead of straight. It is possible that horn-core shape evolves during the Hadar Formation from the condition of rather low insertions, little curvature or distal divergence and slight medio-lateral compression to more upright insertions, a forwardly curved course with clockwise torsion on the right side, stronger distal divergence, and slight antero-posterior compression. It is also possible that the braincase shortens and that the slight indication of a parietal boss disappears altogether, but these are not very certain. There also seem to be evolutionary changes at the back of the skull in the Afar alcelaphines. In AL 208-7 and AL 353-3 the junction between the base of the nuchal crest and the back of the zygomatic arch is not posteriorly placed, each side of the occipital surface faces partly laterally as well as backwards, there is a strong median vertical ridge on the occipital, and the mastoid is wholly contained within the occipital surface. These characters are all linked and the converse conditions are found in AL 161-5 and AL 310-18 in which the junction of nuchal crest and zygomatic arch is more posterior, the occipital faces more wholly backwards and has less of a median vertical ridge, and the lateral parts of the mastoids have the appearance of being deflected to face laterally just in front of the occipital edge. AL 161-5 and AL 310-18 are closer to extant *Alcelaphus* and many *Damaliscus* and one imagines that they are more highly evolved.

These Pliocene alcelaphines differ strikingly from extant *Alcelaphus* by the absence of extreme braincase shortening and face lengthening, more extensive

preorbital fossae, and the absence of horn-core specializations as well as by more minor characters. They also show differences from *Damaliscus*: transverse ridges usually absent on the horn-cores, the horn-core compression evolving to become slightly anteroposterior rather than slightly mediolateral, horn-cores not curved backward, horn-cores more divergent distally (not a difference from *D. lunatus lunatus*), the diminishing parietal boss, the braincase roof not curved in profile, the external auditory meatus set lower in relation to the occipital surface behind it than in male *D. lunatus*, a narrower basioccipital, and the suture at the back of the parietal protruding further forwards in its central parts (not a difference from *D. dorcas*). They differ from both *Alcelaphus* and *Damaliscus* by the angled ventral border of the mastoid.

The teeth of the Afar alcelaphines differ from extant alcelaphines by their more primitive characters. They are probably less hypsodont; on the upper molars the central cavities are less complicated, the ribs are less prominent in relation to the styles, the medial lobes are perhaps less rounded; on the lower molars the central cavities are less curved and the medial walls perhaps less outbowed; on P_4 the rear part (the region of the hypoconid, entoconid and entostylid) is less reduced, and the valley between entoconid and entostylid is perhaps oriented more nearly transversely. Insufficient of them are known for the reduction or otherwise of P_2 to be assessed.

Both species of *Damalacra* differ from the Hadar Formation species by slightly smaller size, horn-cores probably longer and with bases not usually squared off posteromedially, dorsal orbital rims more strongly projecting, braincase sides parallel and supraorbital pits closer together. Both species would probably also differ in shorter and wider nasals, a less deep face and a more posterior setting of the tooth-row—characters which are so far known only from a unique face of *D. neanica*.

Nearly all the characters mentioned so far are likely to be primitive. *D. neanica* differs additionally from the Afar species in the more posterior insertions and weak anti-clockwise torsion of the horn-cores, and the more inclined braincase roof without a hint of a parietal boss. These characters remove *D. neanica* from likely ancestry to the Afar species. *D. acalla* differs additionally by sometimes showing a flattened lateral surface of its horn-cores, sometimes having a localized swelling at the base of the horn-cores, with more definite backward curvature and pedicels of about equal height on their lateral and medial sides. The last two characters are probably primitive in the Langebaanweg form and the first two, even if advanced, do not appear very imposing.

The Langebaanweg alcelaphine teeth as a whole differ from the Hadar Formation ones by being still more primitive. They are definitely less hypsodont, small basal pillars exist on M_1 s and dP_4 s and occasionally on upper molars, the central cavities of the upper molars are even less complicated, the ribs still weaker in relation to the styles, and the medial lobes are pointed rather than rounded. The medial walls of the lower molars are straighter, the central cavities not very curved and with almost no transverse constriction centrally (except

perhaps in later wear), and the lateral lobes are more pointed. The P_4 has poorer fusion between metaconid and paraconid, a larger rear part, and the valley between entoconid and entostylid is oriented transversely.

Some characters of horn-cores and braincase were mentioned earlier as possibly undergoing change during the span of the Hadar Formation. *Damalaera acalla* is more like the earlier than the later form except in its more upright horn-core insertions. *D. neanica* is more like the earlier in its occipital characters but more like the later in its horn-core characters and complete absence of a parietal boss.

A partial cranium from the Laetolil or Ndolanya Beds, 1959.233 (Gentry & Gentry 1978, pl. 22 (fig. 1)) at present in Nairobi, could be conspecific or a close relative of the Afar species, and *Damalops palaeindicus* (Falconer), 1859, from the Pinjor Formation of the Siwaliks and Tadzhikistan (Dmitrieva 1977) could also be a close relative. Details of *D. palaeindicus* are given in Lydekker (1886, pl. 4 (figs 3, 3a, 5)) and Pilgrim (1939: 67–70), and it was discussed by Gentry & Gentry (1978: 406, 412) in comparison with Olduvai alcelaphines. *D. palaeindicus* differs from the Afar species in that its horn-cores curve backward, they show no rapid tapering above the base and the sides of the braincase appear to be parallel instead of showing posterior widening. The horn-cores may be longer, the braincase shorter, and the tooth-row positioned more anteriorly, but this is not certain. So far as can be seen, the Laetoli specimen agrees more closely with the Afar species than with *D. palaeindicus*. It is apparent that both species of *Damalaera* will differ from *Damalops* about as much as from the Afar alcelaphine.

Apart from the Afar alcelaphine and its possible close relatives, a smaller alcelaphine is represented at Laetoli by a cranium with horn-cores, 1959.277 at present in Nairobi, discussed by Gentry & Gentry (1978: 382, pl. 21, pl. 22 (fig. 2)) who thought it was an early *Parmularius*. Since 1974 some conspecific horn-cores have been recovered from the Laetolil Beds by M. D. Leakey, so it can be taken as a member of the fauna dating from before 3.5 m.y. It differs from the Hadar Formation species by smaller size, possibly longer horn-cores, backward curvature and little distal divergence of the horn-cores, less definite posteromedial squaring off at the horn-core bases, occipital perhaps facing even more strongly laterally on each side, closer supraorbital pits with a more concave area of the frontals in between them, and dorsal orbital rims projecting more strongly as a separate structure from the lateral sides of the horn pedicels, all of which could be conceived as primitive. The slight mediolateral compression and absence of rapid tapering of the horn-cores is more like earlier than later Afar specimens and could also be primitive. Such primitive characters can be attributed either to the greater geological age of the Laetoli species or to its smaller size. Other differences are quite a sharp backwards bend of the horn-core just over half-way from base to tip, a posterolateral basal swelling on the horn-core, higher pedicels, parallel sides of the braincase and a more prominent parietal boss. Some of these may be advanced and others primitive.

The parietal boss and the sharp bend, basal swelling and high pedicels of the horn-cores could all foreshadow *Parmularius* and suggest ancestry to it.

Damalacra neanica horn-cores differ from the Laetoli species by the slight anteroposterior compression, their more posterior insertions, no backward curvature and more distal divergence which appear to constitute their own set of advanced characters. They also lack the sharp alteration in course, a localized basal swelling and high pedicels—the supposed advanced characters of the Laetoli species. The cranial roof is also quite different in *D. neanica* by being shorter, more inclined, straight and without a parietal boss. *Damalacra acalla* horn-cores differ by sometimes having a flattened lateral surface, which may be advanced but is unlikely to be a constant or evolutionarily irreversible character. They also lack some advanced characters of the Laetoli species: the sharp alteration in course, high pedicels, and a strong difference between the heights of the pedicel on its medial and lateral sides. Their basal swelling is not always present nor is it localized posterolaterally. The parietal boss is less obvious. It should also be reiterated that alcelaphine teeth from Langebaanweg are definitely more primitive than those from the Laetoli Beds. Once again *D. acalla* is better fitted for ancestry than *D. neanica*.

The condition of the alcelaphine teeth at Langebaanweg indicates that *Damalacra* is more primitive than the alcelaphines hitherto considered from the Hadar Formation, Siwaliks or the Laetoli Beds. The clear implication is that *Damalacra* at Langebaanweg existed in an earlier time span. *D. neanica* had acquired some specializations of its own which make it unlikely to be ancestral to these forms. It was probably the end of an evolutionary line and it would be unwise to use its advanced characters to look for relationships with later alcelaphines (cf. Gentry in Hendey 1970: 116 in which *D. neanica* was confused with advanced *Parmularius*). The combination of some specializations of the horn-cores with an otherwise primitive skull is analogous to the living *Connochaetes gnou* which, despite its advanced horn-cores, has a short face and teeth which are occlusally simpler than other comparably-sized extant alcelaphines. One imagines that such combinations may have arisen with some frequency in alcelaphine evolution.

There is some reason to believe that alcelaphine horn-core characters can change relatively rapidly. A possible interpretation of events in the Hadar Formation is the evolution of more upright insertions, more forward curvature, more distal divergence and a small degree of anteroposterior compression, all of which are a repeat of characters which had already appeared in *Damalacra neanica*. Even at Langebaanweg itself *D. acalla* horn-cores of bed 3aN seem to be losing their backward curvature and acquiring more divergence distally, almost in imitation of the *D. neanica* which had been so abundant in bed 3aS.

It is interesting that a *Damalacra acalla* horn-core such as L30215 in bed 3aN not only has a degree of distal divergence and little backward curvature, but also a base which has become squared off posteromedially, all of which foreshadow the Afar alcelaphine. The tendency of horn-cores to become

shorter from 3aS to 3aN could also be a means for them acquiring a more tapered appearance like the Afar alcelaphine. It is wise not to read too much into these supposed tendencies. More material from Langebaanweg is still being accessioned at the South African Museum and will provide a basis for a more thorough examination. One can have little confidence that all alcelaphine horn-core characters are stable or that, once acquired, they need be irreversible. However, it is unquestionable that *Damalacra acalla*, particularly as known from bed 3aS, is better fitted than *D. neanica* to be an ancestor of later alcelaphines by reason of its lack of specialized characters. Its only known locality at the southern end of Africa is an unlikely venue for evolutionary enterprise, but *D. acalla* or a closely related species further north in Africa is potentially an ancestor for the Afar alcelaphine and even for other species such as the Laetoli species represented by the cranium 1959.277.

As yet there is little evidence of *Damalacra*-like alcelaphines further north in Africa. But there is some. A horn-core cast from Wadi Natrun, BM(NH) M8199, is the base of a much damaged horn-core, probably of the right side, and appears to be the one mentioned by Studer (1898: 76) and Andrews (1902: 438). It is labelled *Hippotragus ?cordieri*, but could belong to a *Damalacra*. A left upper molar from Garet el Muluk at Wadi Natrun figured by Stromer (1907: 120, pl. 20 (fig. 1)) and identified by him as perhaps tragelaphine, appears to represent an alcelaphine at an evolutionary level comparable with *Damalacra*. Its basal length is given as 21 mm. A cast of a left M_3 also from Wadi Natrun, BM(NH) M 12361, which Andrews (1902: 439, p. 21 (fig. 9)) thought was from a large gazelle-like form, could also represent an alcelaphine at the *Damalacra* level. Its occlusal length is 28,3 and its height (early wear) is c. 32 mm.

It begins to look as if the evolutionary history of medium sized alcelaphines has been of successive replacements of one dominant group by another. One could conjecture that the living *Alcelaphus* and *Damaliscus* have replaced the various *Parmularius* species and *Damaliscus niro* of the Pleistocene. (They could also have come close to replacing *Beatragus* which seems to be a lineage on the verge of extinction.) Now it looks as if *Parmularius* and *Damaliscus niro* themselves had replaced earlier Pliocene alcelaphines such as the Afar species and *Damalops*, while *Damalacra* is giving us the first intimation of a still older stratum of alcelaphines. The actual phylogenetic path from one dominant group to its successor is still a conjectural matter. *Parmularius* can be convincingly derived from Laetoli 1959.277, but *Damaliscus* and *Alcelaphus* may come either from this species or from the stock containing the Afar species and *Damalops palaeindicus*. There is a possibility that the Afar species and *Damalops palaeindicus* are a Pliocene dispersal not ancestral to any later forms. It has been noted above that they could be descended from *Damalacra acalla* or some more northern *Damalacra* species, and it is also possible that 1959.277 has a similar ancestry.

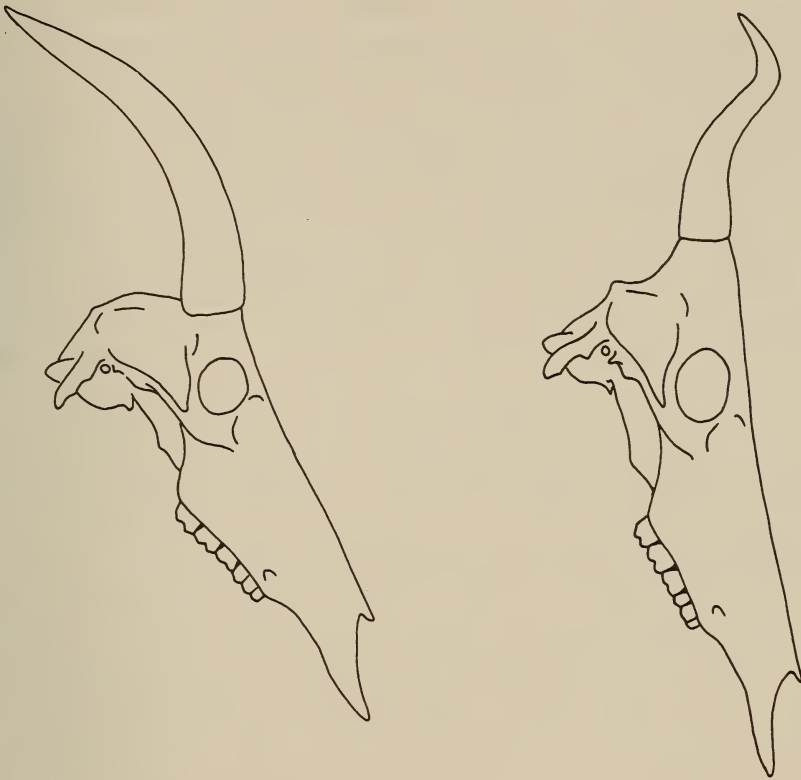


Fig. 51. Lateral views of skulls and horn-cores of *Damaliscus lunatus* (left) and *Alcelaphus buselaphus* (right), shown at their normal inclinations when not feeding.

Functional skull morphology and evolution in alcelaphines

The two functions which mainly lead to variation of skull morphology among bovids are feeding (ingestion and mastication) and horn support. Other functions, such as breathing or input of sensory information, must not be impaired by changes in feeding habits or horn support, but are not themselves the cause of larger scale morphological changes. In living *Damaliscus* and *Alcelaphus* (Fig. 51) the most notable feature of the skull is the long face. The most likely explanation for this is that animals grazing at ground level need to have eyes as high as possible to avoid being surprised by predators. In line with this requirement they also show long diastemata, tooth-row forward of orbital level (especially in *Alcelaphus*), and the brain cavity becoming realigned diagonally instead of horizontally. When not feeding, *Alcelaphus*, and to a lesser extent *Damaliscus*, hold their heads more nearly vertical than non-alcelaphine antelopes. (When asleep while standing (Plessis 1972, fig. 11) their heads can swing even further to an almost inverted position.) This is mechanically more

convenient with long skulls in which the entire weight has to be supported on the rest of the body at the occipital condyles, and it also causes less obstruction to the field of vision. It is desirable in bovids for the horn-core insertions to be as high as possible on the skull, presumably to ensure maximum visual effect. Consequently, an antelope with a long face held vertically could well have insertions in an extreme position behind (now = above) the orbits. This has happened in *Alcelaphus buselaphus* where the insertions are close together on a united pedicel, and in *A. lichtensteini* where they are wide apart but also high. The changed position of the insertions is also linked with horn-core curvature being forward rather than backward. This is a means of ensuring that the distribution of weight in relation to the condyles continues to be balanced. If a *Damaliscus* evolved posterior/high insertions like *Alcelaphus*, then it would have to evolve either a more vertical carriage of its head or forward curvature of its horn-cores to avoid a weight imbalance on the occipital condyles. It is difficult to assess how the different structure of the horns in *Alcelaphus* and *Damaliscus* affects dominance-testing encounters between conspecific males. In high intensity exchanges *Damaliscus* kneels on its carpal joints, may even hold its forehead to the ground and the horns of the opponents interlock (David 1973, fig. 11f; Lynch 1974: 37; Monfort-Braham 1975, fig. 6). *Alcelaphus* also locks horns but they do not appear to get to the stage of pressing their foreheads to the ground. The tips of all *Alcelaphus* horn-sheaths are turned backward, unlike *Damaliscus*, so in this position *Alcelaphus* would more readily injure one another. Walther (1972: 403) notes that hartebeests do injure themselves more often than most other horned ungulates, so perhaps this is what actually happens.

It is apparent from the foregoing comments that the major differences between *Damaliscus* and *Alcelaphus* skulls are a single suite of functionally and mechanically linked characters. This must apply also to the differences of *Damalacra neanica* from *D. acalla*. There must have been ecological opportunity for two species to coexist, just as at the present day, and one of them evolved similar but less extreme differentiating characters of posterior horn-core insertions, shortened and inclined braincase roof, horn-cores curving less backward and even forward, and horn-core compression being more anteroposterior than mediolateral. It may be that pairs of sympatric alcelaphines have repeatedly evolved similar differentiating characters. In middle and upper Bed II at Olduvai Gorge *Parmularius angusticornis* had a very short braincase and horn-cores which lack backward curvature. *Damaliscus niro* in the same deposits had backwardly curved horn-cores and may also have had a longer braincase. If the above reasoning is correct then early alcelaphines at Langebaanweg had already become grazers at ground level. This conclusion is compatible with the presence of horn-cores in female *Damalacra*. It seems from extant bovids that horned females are more characteristic of larger than smaller species and that in Africa horned females are more frequent in species living in open habitats.

Comparison of Langebaanweg alcelaphines with early caprines

The early caprine *Pachytragus* is known from the Turolian fauna of Samos, Greece, where it has two species, *P. crassicornis* and *P. laticeps*, discussed by Gentry (1971). *Pachytragus* shares with *Damalacra* the basic characters of aegodont antelopes such as the rather narrow skull, inclined braincase roof, hypsodonty of the cheek teeth, reduction of basal pillars on the molars and shortening of the premolar row. *P. crassicornis* and *D. neanica* are easily differentiated by a number of individual specializations, but *P. laticeps* and *D. acalla* are morphologically more primitive, and it is necessary to point out how they differ enough to avoid being placed in one genus. *D. acalla* shows:

1. A tendency to basal thickening of its horn-cores usually on the medial surface
2. Its horn-cores are less compressed mediolaterally
3. Their distance apart, measured across the lateral sides of the pedicels, is greater; this character is probably linked with the last
4. The internal hollowing of the horn pedicels has been carried much further
5. The frontals are more raised between the horn-core bases (linked with the last character)
6. The midfrontals suture is less complex and less raised into a ridge
7. The supraorbital pits are smaller
8. The supraorbital pits are situated more widely apart
9. The back of the braincase is wider
10. The occiput is lower
11. The mastoid is probably larger
12. The lower molars have less flattening of their medial walls
13. The P_2 is more strongly reduced

Characters 1, 4, 5 and 13 look like specializations in *D. acalla* and, on the hypothesis that Langebaanweg is the younger site, could have been acquired during descent from an earlier *Pachytragus*. Characters 2, 3, 6, and 12 seem to be specializations in *P. laticeps* and to indicate a different direction of evolution from *Damalacra*. In the case of 7 to 11 either species could show the more advanced condition, nevertheless the characters add to the 'morphological distance' between the two species. The total morphological difference between the two species is too great for them to be regarded as congeneric. Their common ancestry, if one assumes the monophylety of aegodont antelopes, must lie further back in time.

Tribe Neotragini

Genus *Raphicerus* H. Smith, 1827*Type species*

Raphicerus campestris (Thunberg).

Generic diagnosis

Moderate sized to large neotragines. Horn-cores short to moderately long

with little mediolateral compression, inserted widely apart above the back of the orbits, parallel to one another, and having a slightly concave front edge in profile. Postcornual fossa present. Supraorbital pits wide apart, back of braincase roof not very strongly turned down, temporal lines wide posteriorly on cranial roof, preorbital fossa moderate sized to large, premaxilla wide and rising to contact nasals, auditory bulla inflated, median indentation at back of palate level with or forward of lateral ones, palatal ridges on maxilla anterior to the tooth row approach one another closely. Upper molars with quite small styles, central cavities of lower molars disappear early in wear, medial walls of lower molars fairly flat and metastylids not strong, M_3 s with moderate to large back lobes. Metaconid of P_4 passes transversely then backwards, front of lateral wall of P_4 bends round into a transverse plane, P_2 not greatly reduced.

Remarks

The type species occurs in most of southern Africa and Rhodesia, and also in Tanzania and Kenya. There are two other living species, *R. melanotis* (Thunberg) which is largely confined to the Cape Biotic Zone of South Africa, and *R. sharpei* O. Thomas found in Mozambique, Malawi, Rhodesia, Zambia and parts of surrounding countries. Klein (1976) has shown that *R. melanotis* and *R. campestris* were already separate species in the early Upper Pleistocene of the southern Cape Province. *R. campestris* lives in more open country than the other two species and grazes more frequently (Klein 1976: 171–172 and references).

Raphicerus paralius sp. nov.

Figs 52–53, 55–57

?*Madoqua* sp. Gentry in Hendey 1970: 116.

Holotype

L12238—right horn-core, index $15,5 \times 15,2$, and associated right maxilla with P^3 – M^3 in early middle wear (Fig. 52).

Referred material

From QSM:

L21143, L21146 (Fig. 53)—left horn-cores, $18,1 \times 14,7$ and length *c.* 53,0, $17,3 \times 16,2$

L22504, L41606—right horn-cores, $15,7 \times 16,0$, $17,6 \times 17,2$

L41643—left and right horn-cores, the left with an index $17,4 \times 15,6$, also another left horn-core with index $19,7 \times 19,2$

L12513—left and right maxillae with P^3 – M^3 and P^2 – P^4 respectively in early middle wear

L22635—left upper molar

L41607—right maxilla with damaged P^3 – M^2

L41645—right mandible with M_2 and M_3 in early middle wear

L41666—left mandible with dP_4 in early middle wear

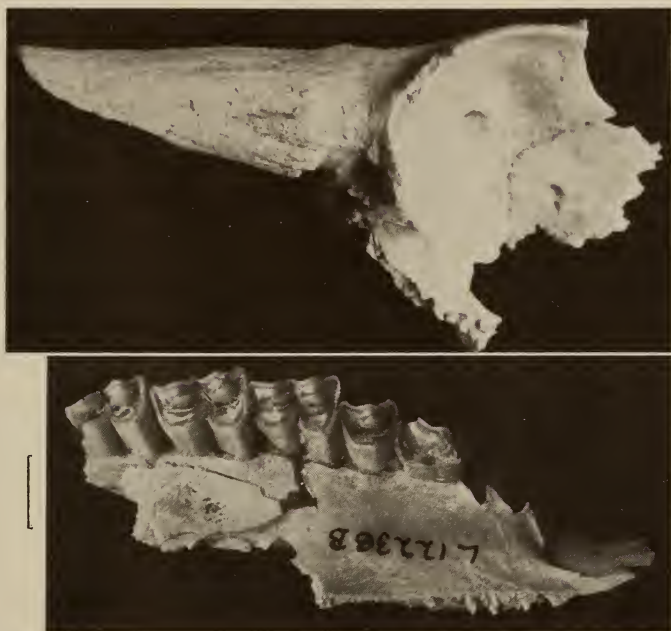


Fig. 52. *Raphicerus paralius*. L12238, holotype. Ventrolateral view of right horn-core. Ventral view of most of right palate and right cheek tooth-row. Scale = 10 mm.



Fig. 53. *Raphicerus paralius*. L21146, L6565, anterior views of left horn-cores. Scale = 10 mm.

Probably from QSM:

L41703—right horn-core, $17,8 \times 13,4$ and length 67,6

From bed 3aS:

L40413—right horn-core, $17,3 \times 16,7$

L40132A—left maxilla with dP^3-M^1

L40270—left mandible with dP_4-M_2

L40443—left maxilla with P^3-M^3 and associated right upper teeth in late middle wear

L41245—left mandible with M_1-M_3 , part of right mandible in early wear (Figs 55, 57)

L41320—right mandible with P_3-M_3 in early middle wear (Fig. 56)

L41526—two left upper molars, left lower molar, other teeth

L40088—right radius with proximal surface and most of shaft (Fig. 21)

L40021—complete left radius with length and least transverse thickness of $145 \times 14,9$ mm

Probably from bed 3aS:

L10788, L10789, L10931—right upper molars

L10790—left upper molar

L11008—right M_3

L11197, L11198—left lower molar, right dP^3

Probably from bed 3aS, but a few possibly from QSM:

L5412, L6565 (Fig. 53), L6566, L6573—left horn-cores, $20,1 \times 16,2$, $20,4 \times 17,8$, $15,0 \times 13,7$, $16,3 \times 16,2$

L6567—left horn-core

L2931—right horn-core, $18,4 \times 18,2$

L3132—right upper molar

L5312—right mandible with damaged M_1-M_3

L6600—left mandible with M_2 and M_3

From QSM or bed 3aS:

L11157—right horn-core, $17,1 \times 15,7$

L11978—left mandible with M_3

L41686—fragmentary right and left dP^2 s

L9939—distal left humerus

L41684—distal right tibia, partial left naviculocuboid, proximal left metatarsal, much of distal right radius, fragmentary distal metacarpal, terminal phalanx (Fig. 21). All associated with a pair of *Raphicerus* horn-cores but the distal tibia, naviculocuboid and proximal metatarsal are from a larger animal than the distal radius and metacarpal. Also one side of a juvenile distal metapodial which must be a third individual

From bed 3aN:

L45170—right mandible with remains of dP_2-dP_4 in early middle wear above P_2-P_4 , M_1 and M_2

From QSM or bed 3aN:

L40787—distal left humerus (Fig. 21)

Horizon

The holotype comes from the QSM. The species is almost confined to the QSM and bed 3aS of the PPM.

Diagnosis

A *Raphicerus* considerably larger than the three living species. Horn-cores short and thickened basally, generally with a posterolateral keel, a tendency towards a longitudinal concavity in front of it on the posterior half of the lateral surface, sometimes a medial or anteromedial keel and other irregular ridges all of which combine to give an irregularly shaped cross-section. Insertions of horn-cores at a lower angle than in living *Raphicerus*. Postcornual fossa well marked. Supraorbital pits not obscured by overgrowth of the frontals. Preorbital fossa large and deep. Infraorbital foramen above P^2 or the front part of P^3 . Basal pillars present on M_1 and traces of them on other lower molars. Premolar row long. P^2 and P^3 larger than in living *Raphicerus*. Short diastema.

Etymology

The specific name comes from the Greek *paralios*, by the sea, and refers to the type locality for this species being in a coastal region.

Remarks

These fossils are larger than any living neotragine. There is no evidence from the horn-cores (Fig. 54) of a size increase having taken place from the QSM to the PPM. The horn-cores are nearly as short as in *R. sharpei*. Their keels and irregular cross-section are more pronounced than in any other *Raphicerus*, but this may be an allometric feature of large horn-cores in the Neotragini, as indicated more faintly in larger examples of *Neotragus*, *Dorcatragus* and *Oreotragus*. The large and deep or moderately deep postcornual fossae are most like *R. campestris* among living species. There are no sinuses in the frontals. The triangular supraorbital pit is large but shallow round the two foramina in L12238A, but in L6565 and L41643 the pits are smaller and have more resemblance to later *Raphicerus*. The absence of overgrowth by the frontals is like *R. sharpei* and unlike *R. campestris* or *melanotis*. The lowness of the horn-core insertions is only apparent from a few specimens, e.g. L21146, L41606, and the left side of L41643, in which sufficient of the frontals posteromedially to the horn-core has been preserved to show a somewhat *Madoqua*-like aspect of the insertion. Such low insertion angles are more unlike *R. campestris* than *R. melanotis* or *sharpei*.

The maxillae L12238 and L12513B show that there was probably a large and deep preorbital fossa which evidently passed low on the face and far anteriorly. This large fossa would be a resemblance to *R. melanotis*. The infraorbital foramen is low over the back of P^2 or front of P^3 , unlike most *R. sharpei* but resembling *R. campestris* and *melanotis*. The palatal ridges in front of the

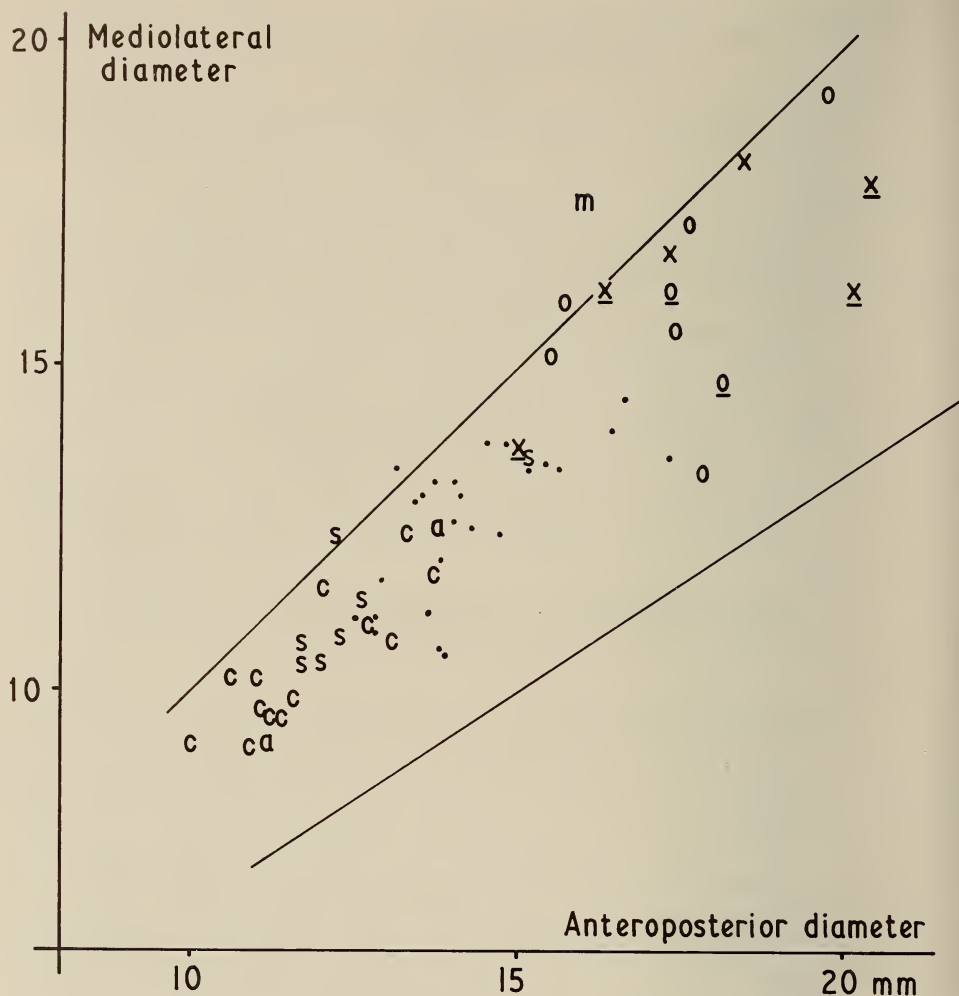


Fig. 54. Basal diameters of neotragine horn-cores. O = *Raphicerus paralius* from QSM, X = the same from bed 3aS; underlined readings are lefts, others rights. a = *Raphicerus* from lower assemblage in Baard's Quarry, m = Makapansgat Limeworks, s = *R. melanotis* from Swartklip, c = extant *R. campestris*, dots = Elandsfontein *Raphicerus* sp. of the right side. Upper diagonal line = 100%, lower one = 66,7% as in Figure 3.

tooth-row on the maxilla L12238 converged and touched at the midline. Judged by its sockets, the missing P² was a large tooth on L12238, as it is on L12513B where it is still present. P³ was also large. The large size of these anterior pre-molars is reminiscent of *Madoqua* or *Raphicerus melanotis* and *sharpei*.

It is not easy to distinguish the teeth of *Raphicerus paralius* from those of the gazelle at Langebaanweg. This problem will be discussed on page 313. The teeth accepted as neotragine show the following characters. They are large



Fig. 55. *Raphicerus paralius*, L41245, left lower dentition in occlusal view. *Gazella* sp., L40603, right lower dentition in occlusal view. Scale = 10 mm.

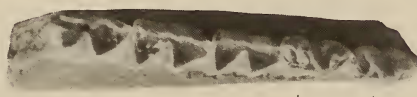


Fig. 56. *Raphicerus paralius*, L41320, right lower dentition in occlusal view. Scale = 10 mm.



Fig. 57. *Raphicerus paralius*, L41245, left mandible in lateral view. *Gazella* sp., L40603, right mandible in lateral view. Scale = 10 mm.

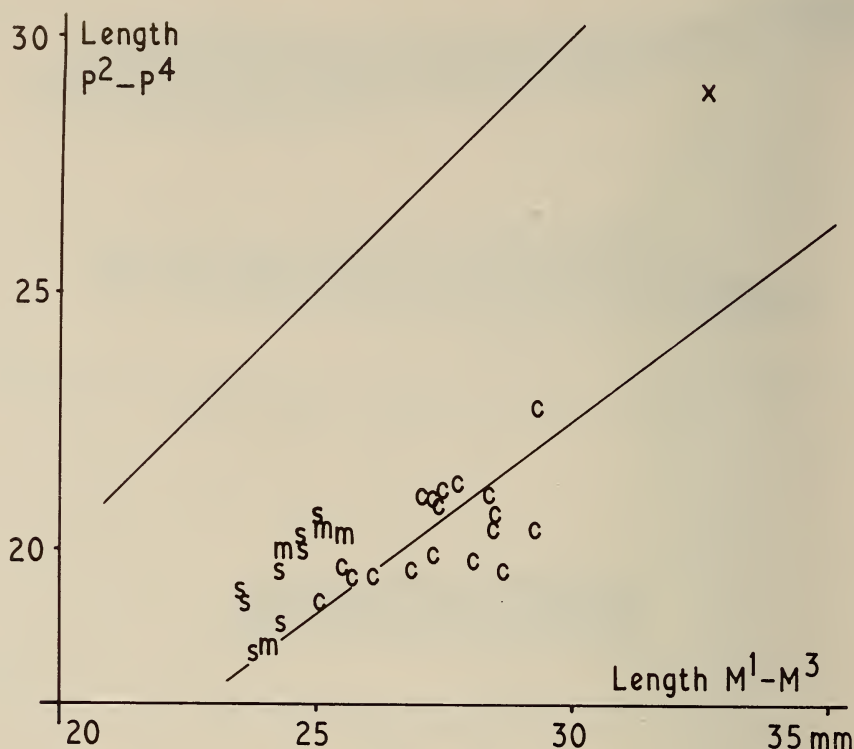


Fig. 58. Occlusal lengths of upper premolar and molar rows in Neotragini. X = *Raphicerus paralius* L12513 from QSM Langebaanweg, C = extant *R. campestris*, m = extant *R. melanotis*, S = extant *R. sharpei*. Upper diagonal line = 100%, lower one = 75% as in Figure 3.

compared with living neotragines (Fig. 58). The upper molars have quite small styles. On the lower molars the central cavities disappear early in wear, the lateral lobes are only drawn out a little in a transverse direction, the medial walls are fairly flat, and metastylids are not strong. There are small basal pillars on M_1 and sometimes persistent traces of the basal pillars on other molars as in L11978. The rear lobe on M_3 is small to moderate sized and in three out of four specimens it shows a flange posteriorly. The premolar row is rather long as deduced from a number of incomplete specimens. On P_4 the hypoconid projects slightly, the metaconid tends to be oriented transversely in its lateral part, the paraconid is joined to the parastylid and shows no approach towards the metaconid behind it, and the front of the lateral wall of the tooth tends to bend round into a transverse plane. The metaconid tends to be in a transverse plane (at least in early wear) in P_3 as well. The P_2 is large and shows little sign of having been reduced in size. The diastema is short and curved upwards and the lower edge of the mandible is curved. Nearly all these characters are

very similar to those of living *Raphicerus*. The tendency for the metaconid to be oriented transversely on P_3 as well as P_4 is one of the few resemblances to *R. campestris*. The curved lower edge of the mandible and the long premolar row are both resemblances to *R. melanotis* and *sharpei*. Otherwise the Langebaanweg species differs from *Raphicerus* only in its large size, the presence of basal pillars on M_1 and possibly on more posterior teeth as well, and in its shorter diastema. It differs from other living neotragines as follows. Compared with *Madoqua* it is much larger, basal pillars are present at least on M_1 , M_3 always has a third (rear) lobe, the hypoconid on P_4 projects less than it sometimes can in *Madoqua*, and P_2 is less reduced. It differs from *Neotragus* by much larger size, poorer styles on upper molars, basal pillars present at least on M_1 , normally a flange on the back of M_3 , longer premolar row, the metaconid of P_4 less clearly diagonal, and a short diastema. It differs from *Oreotragus* by being a little larger, basal pillars present at least on M_1 , normally a flange on the back of M_3 , and the metaconid of P_4 less clearly diagonal. It differs from *Dorcatragus* by larger size, longer premolar row, absence of a slight tendency for metaconid and paraconid of P_4 to approach, and a short diastema.

The distal tibia, L41684, has a long medial malleolus in side view; however its main facets are not greatly indented in the middle of their posterior edge so it is unlikely to be of the gazelle. The front facet for the fibula is small but not minute in comparison with the back one, more or less in front of the back one instead of anteromedial to it, and without a deep indentation between it and the back facet. The back of the rear fibula facet is not much anterior to the rear edge of the bone as a whole. The tibiae of three out of four representatives of extant *Raphicerus campestris* were more indented at the back of the articular facets, two of them were more deeply indented between the fibula facets, and one had the front fibula facet sited anteromedially rather than anteriorly to the posterior one. A single example of *Dorcatragus megalotis*, the living beira of Somalia which is about the size of *R. campestris*, has a very small front fibula facet but is otherwise like *R. campestris*. Three examples of *Oreotragus oreotragus*, another living neotragine of about the size of *R. campestris*, tend to have more massive medial malleoli and more attenuated central ones than in either *R. campestris* or the fossil *Raphicerus*. *O. oreotragus* has rather distinctive limb bones, presumably because its preferred habitat is rocky slopes and outcrops.

The metatarsal associated with the tibia L41684 has no longitudinal groove on its anterior surface but some development of a posterior longitudinal groove. The foramen at the top of the posterior surface is set very deeply. The main facet for articulation with the naviculocuboid curves rather strongly upwards at the back and in side view the top articular surface appears far from flat. There is no groove between the front and back naviculocuboid facets, there are clear anterior and medial sides of the main ectocuneiform facet, and there is a swollen rugose area at the top of the medial side of the shaft. The bone may not have been very long when complete. The metatarsals of three *R. campestris* show

more differences from the Langebaanweg fossil than did the tibiae. There is perhaps less development of the posterior longitudinal groove, the foramen at the top of the posterior surface is set less deeply, the main ectocuneiform facet does not show clear medial and anterior edges, there is no swollen rugose area at the top of the medial side of the shaft, and the top of the articular surface as a whole is anteroposteriorly longer. The single *Dorcatragus megalotis* is like the living *Raphicerus* except that the rear of the main naviculocuboid facet is less upcurved and the articular surface consequently appears flatter in medial profile. The three *Oreotragus oreotragus* metatarsals are notably short and have more of a groove behind the main naviculocuboid facet. However, two of them have distinct anterior and medial edges to the main ectocuneiform facet as in the Langebaanweg fossil, and in all three of them the articular surface is even more compressed anteroposteriorly.

On the distal radius L41684 the back of the medial facet for articulating with the scaphoid is not very deep and hence is unlike a gazelle. The cuneiform articulation has quite a large area on the radius. The distal end as a whole looks a little swollen in side view, and the flanges on the anterior surface are wide apart and the surface between them not very hollowed.

The distal end of the complete radius L40021 is larger than that of L41684, but its characters are similar. The articular surface for the lunate is not deeply excavated.

The proximal radius L40088 has hardly any development of a medial rim to its medial facet, the back edge of the lateral facet is not set anteriorly, and the tubercle at the top of its lateral surface is small and situated below the level of the articular facets. The radii of four available examples of *R. campestris* and the single *D. megalotis* have the distal flanges on the anterior surface closer together than in the Langebaanweg fossils but are otherwise similar. The three *O. oreotragus* have even less of a rear medial facet for the scaphoid and a very small or non-existent radial articulation for the cuneiform. However, the anterior flanges are wide and little pronounced as at Langebaanweg.

The distal humeri L9939 and L40787 have slanted not upright condyles, a deep coronoid fossa, only a shallow hollow for the origin of the lateral humero-radial ligament, the posterior ridge for this hollow situated well forward from the rear edge of the bone, and a moderately developed ridge on the lateral surface marking the origin of the extensor carpi radialis.

The humeri of *R. campestris* and *D. megalotis* have a deeper hollow for the lateral humeroradial ligament. Less certain differences are the possibility of more upright condyles, a higher medial condyle, and the ridge demarcating the posterior limit of the origin of the lateral humeroradial ligament being less anteriorly placed. *O. oreotragus* has a distinctive appearance in anterior view by being transversely wide across the medial condyle and by having a low lateral condyle. However, it does have a shallow hollow for the humeroradial ligament and the posterior ridge to this hollow is situated anteriorly.

TABLE 6
Measurements of neotragine and antilopine dentitions.

	<i>Raphicerus paralius</i>										<i>Gazella</i> sp.			
	L12238	L12513	L40443	L6600	L11978	L41245	L41320	L41645	L6286	L6605	L32899	L40383	L40603	L41690
Occlusal length M1-M3
Occlusal length M2	33,8	32,6	34,2	—	35,8	37,3	—	—	—	—	43,5	—	42,3	—
Occlusal length M3	12,2	12,0	11,7	13,0	11,1	12,2	10,7	10,4	—	—	14,1	13,1	13,2	12,0
Occlusal length P2-P4	—	—	—	15,9	14,4	14,6	—	14,2	—	—	18,3	19,2	17,7	—
Occlusal length P2	—	29,0	—	—	—	c. 27,5	—	—	—	—	c. 21,4	—	—	—
Occlusal length P4	—	9,9	—	—	—	6,3	—	—	—	—	—	—	—	—
Occlusal length below M ₁	7,9	8,2	7,2	—	9,1	—	9,6	—	8,7	9,0	—	—	11,3	9,4
Ramus depth below M ₃	—	—	—	—	17,1	19,3	18,1	—	18,2	19,4	17,4	—	18,3	18,7
Ramus depth below M ₃	—	—	—	—	18,8	21,6	—	—	—	—	23,3	21,1	20,7	—

All are lower dentitions except the first three columns for *Raphicerus paralius*.

Other occlusal lengths of *Raphicerus paralius* are: L11008 M₃ 16,0; L41666 dP₄ 12,3; L45170 dP₄ 13,6.

Other occlusal lengths of *Gazella* sp. are: L5765 M₂ c. 14,6; L10896 M₂ 11,4. Ramus depth below M₁ for L10778 is 20,2.

Measurements

Measurements of horn-cores have already been given. Those of teeth are given in Table 6.

Comparisons

The Langebaanweg *Raphicerus* is larger than the living species of that genus. As has been seen, it differs most from *R. campestris* among living species, and rather less from *R. melanotis* or *sharpei*.

It would not be very convincing to link the Langebaanweg with modern *Raphicerus* except by way of congeneric Elandsfontein fossils, comprising one or two crania, some frontlets, many horn-cores and many dentitions. Most of the Elandsfontein horn-cores differ from living species only by their larger size (Fig. 54) and less upright insertions. They often have an approach to a posterolateral keel and the right horn-core on the frontlet SAM-PQ-E14153 has a mid-lateral keel with a longitudinal hollow between it and the posterolateral keel which suggests a link with the Langebaanweg species. Another Elandsfontein horn-core, SAM-PQ-E927, has an anterolateral keel.

A right horn-core from Makapansgat Limeworks, BPI M478, is like those at Langebaanweg and may be identified as *Raphicerus ?paralius*. Its basal index is $16,0 \times 17,5$ and length is 80 mm. It was published as *Cephalophus pricei* by Wells & Cooke (1956: 12, fig. 6), but the tooth-rows assigned to this species by the same authors are from a bushbuck-sized tragelaphine and one of them is the holotype.

A pair of large neotragine horn-cores from member G of the Shungura Formation, Omo 280 71-1168 and 1169, have an index of $18,7 \times 15,9$ and are like *R. paralius* in their shortness, poor degree of compression and irregularly shaped cross-section arising from strong longitudinal ridging and grooving. However, their insertion is at a less low inclination, they show slight backward curvature and the postcornual fossa is weak, so their identification as *Raphicerus* is not very secure. Moreover, neotragine tooth-rows from low in member G which may or may not be conspecific with the horn-cores, e.g. Omo 75i 70-1106 and L 504-4, have smaller teeth than at Langebaanweg and the former specimen is complete enough to show that the premolar row is much shorter.

Tribe Antilopini

Gazella sp.

Figs 55, 57, 59

Material

A number of horn-cores and dentitions belong to a gazelle. The horn-cores and their basal indices are as follows:

From QSM:

	Left	Right
L13208	$14,3 \times 11,4$ (female)	L13984 part of horn-core
L20510	$13,5 \times 11,8$ (female)	

From bed 3aS:

Left		Right	
L40324	26,4 × 20,5	L40097	32,1 × 24,3
L40390	31,8 × 24,0	L40179	30,2 × 24,3
L41325	30,8 × 22,1	L40277	28,6 × 20,5,
L41528	distal part only		length c. 130
		L40389	14,7 × 13,0 (female)

Probably from bed 3aS, but a few possibly from QSM:

Left		Right	
L3351	25,3 × 18,5	L2617	29,7 × 22,2
L3491	30,7 × 20,2 (Fig. 59)	L2620	26,6 × 19,9
L6077	27,7 × 22,6	L3125	28,8 × 22,2
L6078	28,3 × 23,1	L3196	
L6581	24,3 × 19,1	L3206	28,1 × 20,3
L9149	26,3 × 18,4	L3588	
L11985	16,4 × 13,7 (female)	L4740	27,2 × 21,3
		L5921	
		L6578	26,2 × 19,1
		L6580	24,9 × 19,1
		L10694	31,5 × 21,4, length 155
		L11622	28,0 × 21,4
		L12175	22,6 × 18,9



Fig. 59. *Gazella* sp. L3491, left horn-core in anterior and lateral views. Scale = 25 mm.

From bed 3aN:

Left

- L30209 $28,4 \times 19,8$
- L46041 $16,0 \times 13,0$ (female)
- L46066 $31,6 \times 21,4$

A right horn-core L40036, with index $33,1 \times 23,1$, is of unknown provenance.

The dental remains are as follows:

From bed 3aS:

- L13385—left upper molar
- L40226B—two left upper molars
- L40383—left mandible with M_2 – M_3 in early middle wear
- L40603—left and right mandibles, the right with P_3 – M_3 in early middle wear (Figs 55, 57)
- L41690—left mandible with P_3 – M_2 in late middle wear

Probably from bed 3aS:

- L10289—right upper molar with occlusal length 15,4
- L10290—right upper molar with occlusal length 13,8
- L10291—right P^4

(The last three are probably from one individual. The P^4 is unworn, while L10289 which is probably the M^2 is still in early wear)

- L10342—right upper molar with occlusal length 13,4
- L10778—left mandible with M_1 and no central cavities on M_1
- L10797—left upper molar with occlusal length 14,6
- L10896—right mandible with M_1 – M_2 in late wear

Probably from bed 3aS, but possibly from QSM:

- L5765—right mandible with damaged M_1 – M_3 in early middle wear
- L6286—right mandible with P_3 – M_1 in late middle wear (no central cavities on M_1)
- L6605—right mandible with P_4 – M_1 ; wear as for preceding specimen

From bed 3aN:

- L32089—left upper molar
- L32899—right mandible with M_1 – M_3 in early middle wear
- L33624—left upper molar

Horizon

This species is much more abundant in bed 3aS than in bed 3aN or the QSM.

Description

The horn-cores are moderately long, mediolaterally compressed, with a tendency to flattening of the lateral surface, without keels or transverse ridges, inserted fairly uprightly in side view and not far apart in anterior view, not very divergent, and with rather a strong backward curvature. The widest diameter is situated centrally or slightly anteriorly, the deepest longitudinal grooves are

found mainly anteriorly but some are posterior, the boundary between pedicel and horn-core on the lateral surface has a more noticeably diagonal course than in most gazelles, and the postcornual fossa is shallow or only moderately deep. The frontals contain no internal sinuses and the supraorbital pits are moderately sized and narrowly triangular in shape.

One example, L9149, could be less backwardly curved and more medio-laterally compressed than normal, but to place it in a separate species would be too conjectural.

Most of the horn-cores with any preservation of the surrounding area of the frontals, e.g. L40097, L3491 and L9149, show that divergence from the base was less than one would expect, as if pressure had been applied from the antero-lateral side to give a slight inward tilt to the horn-core base. This may be a feature of early gazelle and neotragine horn-cores.

The only male horn-core definitely from the QSM, L13984, is too fragmentary for any conclusions to be drawn about changes from one member to another.

The upper molars have a strong mesostyle with a concave lateral wall between mesostyle and metastyle, and there is an indentation into the central cavity in the rear lobe. The lower molars are not easy to distinguish from those of *Raphicercus paralius* at Langebaanweg and samples are not large.

Those assigned to *Gazella* are only slightly larger than the neotragine. The back lobe of M_3 is probably relatively larger, and it has a central cavity which is lacking in the neotragine. The medial walls of the lower molars are perhaps flatter, and small basal pillars are visible only on M_1 , neither of which are striking differences from the neotragine. The metaconids on P_3 and P_4 tend to be more diagonally aligned and it is not clear that the front of the lateral wall of P_4 bends round transversely. Judged by the size of its root-sockets, P_2 may be more reduced.

Measurements

Measurements on gazelle lower dentitions are given in Table 6.

Comparisons

It is interesting that 'E' Quarry is a site where *Gazella* is quite common but *Antidorcas* is unknown. The *Gazella* is noteworthy in being rather large for its Miocene/Pliocene age. This makes it unlikely to be related to the only other fossil gazelle recorded from the Cape Province—a species from Elandsfontein identical with one at Olduvai Gorge, Tanzania, taken by Gentry & Gentry (1978: 439, 443) to be closely related or ancestral to the living *G. thomsoni* and *G. rufifrons*. Its horn-cores also differ from those of the Elandsfontein species by being more mediolaterally compressed (Fig. 60), more strongly curved backward, and having the pedicel/horn-core boundary set more diagonally on the lateral surface. The supraorbital pits are sometimes narrower.

Since *Gazella* is a long-lasting bovid in the fossil record and has conservative horn-cores, it is difficult to come to conclusions about the relationships of

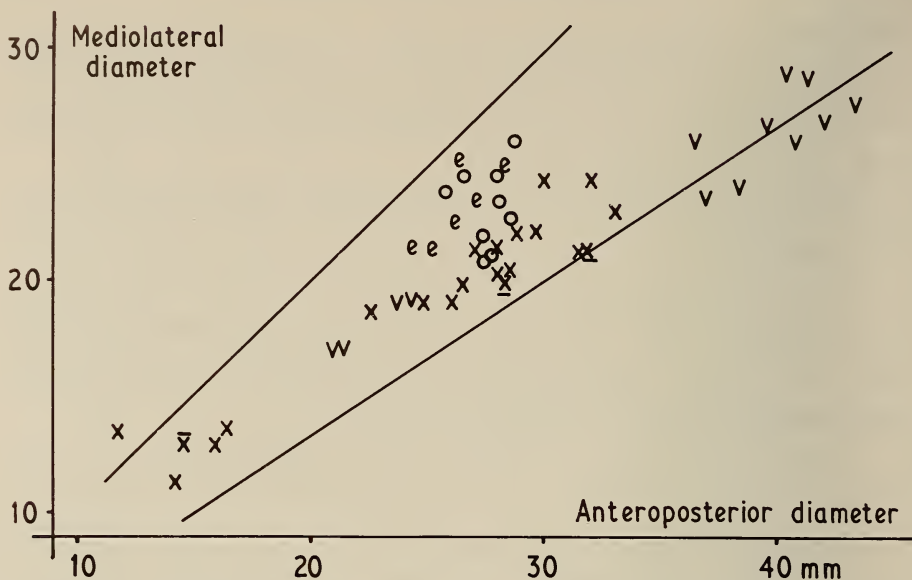


Fig. 60. Basal dimensions of *Gazella* horn-cores. X = bed 3aS Langebaanweg, X = bed 3aN, V = *G. vanhoepeni*, e = *Gazella* sp. from Elandsfontein, O = same species from Olduvai Gorge and Peninj. The lower group of *G. vanhoepeni* are females, previously called *G. gracilior* (see Gentry & Gentry 1978: 440). The lower group of Langebaanweg readings is also of females; all are lefts except X. Male Langebaanweg horn-cores are rights except the two from 3aN. Upper diagonal line = 100%, lower one 66,7% as in Figure 3.

newly discovered forms. However, it is plausible to relate the Langebaanweg species to *Gazella vanhoepeni* (Wells & Cooke 1956) from Makapansgat Lime-works. This latter species was originally put in *Phenacotragus*, a name later recognized to be a junior synonym of *Antidorcas* (Gentry & Gentry 1978: 427). Wells (1969) showed that *G. vanhoepeni* was a gazelle and probably related or ancestral to the three large gazelles still living in Africa, *G. dama*, *G. soemmerringi* and *G. granti*. The horn-cores of the Langebaanweg gazelle are slightly smaller than *G. vanhoepeni*, less long, less markedly curved backward, less strongly compressed, less uprightly inserted, and inserted less closely together. In addition, there is no sign of internal hollowing in the frontals and the post-cornual fossa is shallower. It will be noted that in all these characters the Langebaanweg gazelle can be regarded as less advanced than *G. vanhoepeni* and hence a suitable ancestor for it. Moreover, the leading characteristic of the Langebaanweg gazelle is the strong backward curvature of its horn-cores, and this could foreshadow the even more marked curvature of *G. vanhoepeni*. The diagonal course of the boundary between the top of the pedicel and the base of the horn-core in lateral view is another resemblance between the two species.

A right mandibular fragment with M_3 and partial M_2 from Mpesida (KNM-MP 129) was attributed by Gentry (1978a: 302) to Antilopini, probably *Gazella*, but Thomas (1979b, pl. 2 (fig. 15)) believed that it was equally likely

to be a *Raphicerus*, i.e. neotragine. Its teeth are smaller than the Langebaanweg gazelle and its mandibular ramus is shallower beneath M_3 than in either the Langebaanweg gazelle or neotragine. It is not likely to be conspecific with either.

Tribe Ovibovini

Gen. et spp. indet.

Figs 61–62

Gentry (1971: 289–290) pointed to two stocks of Ovibovini: an earlier group known from the Turolian or equivalent faunas of Eurasia and centred on *Urmiatherium*, and a later group known mainly from the Villafranchian or equivalent faunas of Eurasia and Africa, centred on *Makapania* and *Megalovis*. The second group could perhaps be descended from *Palaeoryx*, a Eurasian contemporary of *Urmiatherium* (Gentry 1971: 281–283), and it also contains the only two living ovibovines, the North American musk ox *Ovibos moschatus* and the takin of Tibet and western China *Budorcas taxicolor*. The extinct group of Turolian ovibovines had some very specialized characters of the horn-cores and of the basicranial region of the skull, and Teilhard de Chardin & Trassaert (1938: 91) have already noted that later ovibovines look less specialized. It is thus difficult to frame a definition embracing both the groups of the tribe. Among their major characters are that they are moderate to large bovids and tend to have narrow and high rather than low and wide skull proportions. Horn-cores are often short, have a tendency to become stumpy or abbreviated, and develop insertion positions behind the level of the orbits. The frontals contain cellular sinuses. The supraorbital pits are small. The braincase is short and its roof usually steeply inclined. The auditory bulla is small. The teeth are hypsodont with reduced or absent basal pillars, and the premolar rows are short.

In the group of later ovibovines there are no keels or transverse ridges on the horn-cores, the horn-cores are often very divergent, the frontals raised between the horn-core bases, the orbital rims strongly projecting, the skull wider across the orbits than across the occipital surface, the temporal lines quite wide apart on the cranial roof, the mastoids usually large, and the basioccipital triangular shaped and with hollows on its surface between the anterior and posterior tuberosities. There may be goat folds on the lower molars, paraconid and metaconid are fused on P_4 , and there is a deep lateral indentation in front of the hypoconid on P_4 .

The best known African ovibovine is *Makapania broomi* Wells & Cooke, 1956, from Makapansgat Limeworks and probably from Sterkfontein Type Site (the teeth of *M.* cf. *broomi* Vrba, 1976: 48), which Gentry (1970b) considered was quite closely related to *Megalovis latifrons* Schaub of the later Villafranchian of Europe. Unpublished or little-known fossils from other Pliocene and Pleistocene sites, including Langebaanweg, show that one or more ovibovine lineages had quite a wide distribution in Africa.

Material

L13105—cranium preserved to just beneath and behind the horn-core insertions and a separate piece of the same individual showing the anterior parts of both frontals and the front surface of the base of the left horn-core. From the QSM (Fig. 61)

L13209—frontlet with horn-core bases, also from the QSM

L41144—shattered left mandible with M_1 , M_2 and unerupted M_3 and a P_4 as a separate piece. It comes from bed 3aS of the PPM. (Fig. 62)

L45104—cranium preserved to a level just behind the horn-core bases. It is unlikely to be conspecific with L13105 or L13209. It comes from bed 3aN

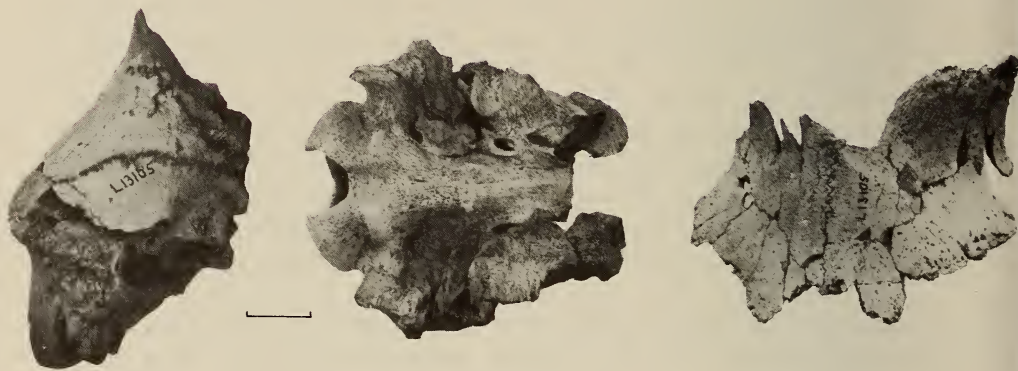


Fig. 61. *Ovibovini* sp. L13105, from the left: cranium in lateral and ventral views, partial frontlet in anterior view. Scale = 25 mm.



Fig. 62. *Ovibovini* sp. L41144, left M_1 and M_2 in occlusal view with M_3 out of alignment behind them. Scale = 10 mm.

Description

On L13105 the horn-core insertions appear to have been close together, the frontals have a well-developed system of internal sinuses, the braincase is rather short and widens posteriorly, the flat-topped cranial roof is steeply angled, the parietofrontals suture is not very complicated and has a forwardly directed central indentation, the temporal ridges do not approach close to one another posteriorly, the occipital has a tendency to a horizontal dorsal edge and shows no median vertically running ridge but does have twin shallow hollows dorsally, and the mastoids were probably of moderate to large size although their lateral parts are now missing along with much of the nuchal crests. The skull would have been wider across its orbits than across the occipital surface. There is a narrow triangular basioccipital with small anterior tuberosities and no longitudinal ridges behind them. A central longitudinal ridge arises just in front of a short groove between the posterior tuberosities and runs through to the basisphenoid, the ridges on the posterior tuberosities are aligned transversely not posterolaterally, the basioccipital is not constricted across its central part, the basisphenoid is not greatly angled on the plane of the basioccipital, and the foramina ovalia are moderate to large sized and situated well forward of the anterior tuberosities.

The separate piece of the same individual shows that there are small supraorbital pits in front of the horn-core bases. The horn-core would have been steeply inserted, the dorsal part of the orbital rim was horizontal and projected quite strongly, and the midfrontals suture is not very complicated at the level of the supraorbital pits.

The frontlet L13209 has the frontals between the horn-core bases raised well above the level of the dorsal part of the orbital rims, and the midfrontals suture is not very complicated. The horn-cores are inserted close together above the back of the orbits and are compressed in the anterolateral to posteromedial plane. They appear to have been moderately divergent and their basal part ascended in a straight line if one can judge from the back surface of the right horn-core. The braincase roof is steeply inclined.

The cranium L45104 is larger than L13105, the braincase roof is angled by reference to the plane of the occipital but less steeply, the parietofrontals suture is straight, there is less obviously a flat top to the occipital surface, there is a median vertical ridge on the occipital, the back part of the frontals is less upwardly slanted on the plane of the braincase roof so that the rise of the (unpreserved) horn-core pedicel would have been further forward, and the basioccipital has larger anterior tuberosities. This puzzling fossil is not definitely ovibovine. It has a less narrowed appearance than L13105, and no information is available about its horn-cores and the frontals area.

Measurements on L13105 and L45104 are:

Width across lateral edges of supraorbital foramina	69,7	—
Maximum braincase width	93,4	107
Occipital height from dorsal edge of foramen magnum	50,5	56,5

Skull width across mastoids behind external auditory

meati	127,3	c. 149
Width across anterior tuberosities of basioccipital . .	19,8	27,2
Width across posterior tuberosities of basioccipital . .	45,1	50,0
Closest approach of temporal lines on cranial roof . .	c. 40,0	54,2

The minimum width across the lateral sides of the horn pedicels on L13209 is 126,7.

The lower molars of L41144 are rather large to agree with the Alcelaphini from 'E' Quarry and too hypsodont to belong to the boselaphine. A goat fold is seen on M_1 , one will appear in later wear on M_2 , but none exists on M_3 . These goat folds are more pronounced than in the Alcelaphini but less than in *Makapania broomi*. Tiny basal pillars occur on M_1 and M_2 ; they are too tall and thin to match the boselaphine and agree better with some individuals of the Langebaanweg alcelaphines than with *M. broomi* which has no basal pillars. The medial walls of the molars are somewhat outbowed between the stylids, agreeing both with Alcelaphini and *M. broomi*. The P_4 has a projecting hypoconid and fusion of paraconid with metaconid, as in the alcelaphines and *M. broomi*. At Makapansgat Limeworks lower molars of *M. broomi* can be distinguished from alcelaphines by their more pointed lateral lobes and flatter medial walls, but these criteria are unavailable with the more primitive alcelaphine teeth at Langebaanweg. It seems very probable that L41144 does belong to the Ovibovini. The occlusal lengths of its teeth are: P_4 14,4, M_1 21,8, M_2 25,8 and M_3 34,6. The crown height of the metastylid of M_3 is c. 40,3.

Comparisons

It can be seen that the combination of characters cited for the QSM fossils fits them to belong to the Ovibovini: moderate size, rather a narrow cranium, greater skull width across orbits than occipital, frontals raised between the horn bases and having cellular sinuses, small supraorbital pits, short braincase with an inclined roof, temporal lines quite wide apart and mastoids probably moderate to large sized.

The most interesting comparison for the QSM ovibovine is naturally with *Makapania broomi*. The latter is fairly well preserved and its localities are not that far across the continent from Langebaanweg. *M. broomi* is about the same size as the Langebaanweg form and similar in that its horn-cores are antero-posteriorly compressed, its frontals raised between the horn-core bases, the braincase short, the parietofrontals suture centrally indented, the supraorbital pits small, the sinuses in the frontals extend to the top of the pedicels, and there is a valley between the posterior tuberosities of the basioccipital which widens posteriorly. *M. broomi* differs by its horn-cores being inserted transversely (= a divergence of nearly 180°) and wider apart, the braincase roof less steeply inclined, the horn-cores inserted further behind the orbits, probably by the presence of a ridge between horn-core and orbital rim, a shorter wider basioccipital, the more complicated morphology of the anterior tuberosities

of the basioccipital, and localized deep hollows posterolaterally to the anterior tuberosities. The divergence and relatively posterior insertion of the horn-cores and the basioccipital characters are probably advanced in *Makapania*, but the steeply inclined braincase of the Langebaanweg ovibovine looks more advanced than *Makapania*.

An unpublished ovibovine skull from the middle or upper Hadar Formation, AL 136-5, agrees with *Makapania broomi* and the QSM form in size. Other similarities to the Langebaanweg form, lacking in *M. broomi*, are the steeply sloping braincase roof (perhaps even more inclined than at Langebaanweg), and insertions above the back of the orbits. However, it differs from Langebaanweg by having massive horn-cores which emerge transversely, frontals even more raised between the horn-cores, a parietofrontals suture which is straight or only slightly indented in its centre, the braincase narrowing instead of widening posteriorly, a median vertical ridge on the occipital, a wider basioccipital, anterior tuberosities of the basioccipital with long sharp ridges converging anteriorly, a central longitudinal groove on the basioccipital, no widening of this groove between the posterior tuberosities, and hollows on the basioccipital surface anterolateral to the posterior tuberosities.

The European species with which the QSM ovibovine can be compared are *Megalovis latifrons* Schaub (1923: 292, fig. 5; 1943: 281, figs 5-6) from the upper Villafranchian of Senèze, France, and *Hesperoceras merlae* Villalta & Crusafont-Pairo (1955: 431, figs 1-3) from the lower Villafranchian of Villaroya, Spain. They differ from the Langebaanweg ovibovine by the braincase not widening posteriorly, its roof being less inclined, the basioccipital being wider and having larger and more rugose anterior tuberosities, and by having hollows on the basioccipital surface. *H. merlae* differs by having the horn-core bases compressed in the anteromedial to posterolateral plane. It also has a median vertical ridge on the occipital and the central longitudinal groove on the basioccipital does not widen posteriorly between the posterior tuberosities. *M. latifrons* differs by the dorsoventral compression of its horn-cores, their more transverse emergence, the ridge between the horn-cores and orbital rims, the frontals not very raised between the horn bases if at all, the more posterior horn-core insertions, the braincase not widening posteriorly and the central longitudinal groove of the basioccipital being present but constricted between the anterior tuberosities.

It likely that the QSM ovibovine is less advanced than the other forms with which it has been compared, in the horn-cores being little divergent and their insertions being less far behind the orbits. Other apparently primitive characters are the basioccipital not being very wide, its small anterior tuberosities, and the absence of hollowings on the surface between the anterior and posterior tuberosities. The basioccipitals of Ovibovini look as if their abundance of morphological detail ought to be informative, but the difficulty with fossils is to guess how much of the variability is individual rather than between species. In essence their basioccipitals are short, wide and triangular and have a central

longitudinal groove. The groove widens posteriorly in the Langebaanweg species, *Makapania broomi* and *Ovibos moschatus* but not in the Afar species, *Hesperoceras merlae* or *Budorcas taxicolor*. It often becomes constricted between the anterior tuberosities, as in *Megalovis latifrons*, and may even become only a minor feature on a longitudinal ridge as in *Makapania* and *Ovibos*. The Langebaanweg species has the ridge alone and not the anterior part of the groove, and the Afar species has no constriction between the anterior tuberosities. The anterior tuberosities are poorly developed in *Budorcas*, perhaps secondarily so, otherwise they are more strongly developed in later ovibovines than in the Langebaanweg species, as also are the surface hollowings between anterior and posterior tuberosities. The morphology of the anterior tuberosities differs much between the species.

At present it looks as if the Afar species is a form in which the raising of the frontals and inclination of the cranial roof has become more accentuated, the horn-cores more massive, at least basally, and the basioccipital has evolved somewhat differently from *Makapania broomi*. The position of the horn insertions above rather than behind the orbits probably arises from the exaggerated raising of the frontals and need not be primitive. That the Langebaanweg form appears so primitive in its basioccipital probably denotes that it is from a fauna earlier than either Afar or Makapansgat Limeworks. The relationships of the Olduvai ovibovine horn-core (Gentry & Gentry 1978: 445, pl. 41) and '*Bos*' *makapaani* Broom (1937: 510) are still puzzling. The relationships of the African Ovibovini as a whole to those of the Villafranchian and later periods in Eurasia also need clarifying.

Two associated limb bones from bed 3aS at Langebaanweg, a right femur and tibia, both numbered L40274, may be ovibovine. They are smaller than in living *Ovibos* or *Budorcas*, with lengths and least transverse thicknesses of $249 \times 24,6$ and $291 \times 23,8$ respectively. The femur shows no indentation between great trochanter and articular head in anterior view, as is also the case in both living species. It also has an anteroposteriorly narrowed lateral part of the articular head, which has, however, reduced the articular head to less of a ball than in either living species. Unlike either living species the great trochanter is not mediolaterally thickened in dorsal view, the vastus lateralis crest passes backwards and is quite sharply outlined, and there is a prominent vertical ridge at the centre top of the anterior surface marking the lateral edge of the vastus medialis and intermedius insertions. The anterior edge of the lateral roughened fossa at its distal end is situated rather posteriorly, but no other characters are like *Budorcas* rather than *Ovibos*. The tibia shows a poorly developed central tubercle and flanking hollows on the proximal articular surface, the lateral edge of the lateral facet is not upturned and distally the medial malleolus is long, like both living ovibovines. Neither the proximal articular surface nor the astragalar facets distally are as wide as in the living ovibovines. A small knob of the proximal articular surface overlaps the top of the posterior surface centrally, unlike the living species. For both bones the

specialized goat-like characters of *Budorcas* limb bones are largely absent.

Enigmatic horn-cores

In any sizeable collection of fossil bovids there are always a few horn-cores difficult or impossible to identify. One pair of such horn-cores in the Langebaanweg collection is L41695 which is long and thin with a basal index of $39,3 \times 32,6$ and a length of 195 mm. One could imagine them as females of one of the alcelaphine species except that they are disproportionately thick at their bases.

Another group of horn-cores (L30885, L40084, and others) remain unidentified. They have rather large internal sinuses passing far up the pedicels and could belong to *Mesembriportax acrae* at an immature growth stage before the anterior keels appear.

BOVIDAE FROM BAARD'S QUARRY

A small number of bovid remains come from Baard's Quarry but are clearly not all from the same time level. By examination of matrix, bone preservation, and from what is known of the geology of the quarry, Hendey (1978a) has separated the fossils as a whole into a 'lower level' assemblage and an appreciably younger 'upper level' one. Both assemblages are younger than the 'E' Quarry fossils. It must be stressed in Hendey's (1978a: 4) words that 'almost all the fossils from Baard's Quarry were collected after the deposits in which they occurred had been moved by the mining operation and consequently the provenance of specimens has for the most part to be inferred'.

Tribe Boselaphini

Lower assemblage

L1588A is a left horn-core fragment about 90 mm long, not distinguishable on what has been preserved from *Mesembriportax acrae*. The top of the anterior keel is present and there are deep longitudinal grooves on the posterior surface.

Tribe Reduncini

Lower assemblage

The following horn-cores are reduncine:

L565	left, $32,7 \times 26,4$ (Fig. 63)	L564	right, probably the same individual as L565
L1521B	left, $31,6 \times 27,6$	L1378A	right, could be the same individual as L1603
L1570A	left	L1521A	right, probably the same individual as L1521B (Fig. 63)
L1588B	left, $30,9 \times 26,2$		
L1603	left, $32,5 \times 27,0$		

About eighteen poorly preserved fragments of horn-cores, the majority of the total known from Baard's Quarry, are also likely to be of this species.



Fig. 63. *Kobus ?porrecticornis* from Baard's Quarry. L564, anterior view of right horn-core. L1521A, lateral view and cross-section of right horn-core. Lateral side of cross-section towards the left and anterior side towards the base of the illustration. Scale = 25 mm.

These horn-cores were wrongly described as inseparable from *Redunca* (now *Kobus*) *ancystrocerus* by Gentry (in Hendey 1970: 115).

These horn-cores would have been fairly long as shown by L1378A which has a preserved length of 130–140 mm and may have been *c.* 180 mm when complete. They show slight mediolateral compression and a tendency to a flattened lateral surface. The level of the widest transverse diameter lies centrally or anteriorly and there is an approach to a posterolateral keel. This, combined with the slight mediolateral compression, gives the horn-cores a *Kobus*-like rather than a *Redunca*-like aspect. They are inserted close together on low pedicels above the orbits, with a moderately strong divergence and gentle, even backward curvature. The divergence lessens from the base upwards. L1378A has greater initial divergence than the other specimens. They have a moderate angle of insertion in side view. There are no transverse ridges, the frontals are slightly higher than the dorsal parts of the orbital rims but not by much, the supraorbital pits are small, the postcornual fossae narrowly triangular but deep, no sinuses are visible within the frontals, and the sulci of the brain surface are like Reduncini rather than Antilopini.

The nearest resemblance of these horn-cores is to a reduncine from the Lukeino Formation (Gentry 1978*a*, 302; Thomas 1979*b*, fig.3) as well as to some Siwaliks Group horn-cores, namely a left horn-core, BM(NH) M 15473, of *Dorcadoxa porrecticornis* (Lydekker 1878: 158), a right horn-core, BM(NH) M 15474, of *Gazella? superba* Pilgrim (1939: 36), and others illustrated by Lydekker (1878, pl. 25 (fig. 4); 1886: 11, fig. 2) and Pilgrim (1939, pl. 1 (figs 4, 4a-b)). The Siwaliks horn-cores were supposed by Pilgrim to be from the Dhok Pathan stage. They were collected at Hasnot, an area where many of the fossils may be from levels slightly younger than the type Dhok Pathan Formation. They can best be referred to *Kobus porrecticornis* and Thomas (1979*b*) notes this species as first appearing in the type zone (= upper part) of the Dhok Pathan Formation. The Lukeino reduncine belongs to the same or a closely related species, and Thomas (1979*b*, pl. 2 (fig. 13)) further records it at Mpesida on horn-cores which Gentry (1978*a*: 302) had taken as tribe indeterminate. The Baard's Quarry examples differ from *K. porrecticornis* and the African *K. aff. porrecticornis* only by being slightly smaller and having smaller supraorbital pits. An unpublished pair of horn-cores, AL 99-3, 43, from the Amado Formation, Afar, are very similar to the Siwaliks horn-cores, but their midfrontals suture is deeper in section. Their supraorbital pits also are larger than at Baard's Quarry. If the Baard's Quarry fossils were conspecific with the Lukeino and Siwaliks ones, there would be an implication of a geological age between 3.0 and 6.7 m.y., but the small supraorbital pits may denote a different species.

The Baard's Quarry specimens differ from some horn-cores of a supposed early kob in member B of the Shungura Formation, e.g. L1-24 and L1-189, by being more compressed mediolaterally, without transverse ridges, inserted closer together and more uprightly, with less divergence basally and with lessening divergence distally. They differ from *Kobus subdolus* and *Kobus* sp. 2 of 'E' Quarry by being smaller, without transverse ridges, more uprightly inserted in side view, with more of a backward curvature, and with smaller supraorbital pits. They are longer and more divergent than *K. subdolus* and have a more definite distal lessening of their divergence than in *Kobus* sp. 2.

One does not know whether or not the Baard's Quarry and similar Lukeino and Siwaliks horn-cores are related to modern reduncines. It is difficult to decide about the primitive and advanced conditions for the characters of transverse ridges, inclination and divergence, and it would be presumptuous to assert that evolutionary sequences for such characters had been 'once only' transitions from the supposed primitive to the advanced. Perhaps *Kobus porrecticornis* was a not very distinctive early relative of *K. kob*, which existed with little change during a long span of time from the latest Miocene to mid Pliocene and, therefore, is of limited use for correlations. Teeth likely to belong to it are more typically reduncine than those of the 'E' Quarry *Kobus*, suggesting either that *K. porrecticornis* occurred later or that, if its early records were contemporaneous with 'E' Quarry, it is a more plausible ancestor of modern species.

A left lower molar, L1487, from the lower assemblage, is similar to the

teeth numbered L21 and discussed below. It is in early middle wear, its occlusal length is 15,8, and it is a typically reduncine tooth.

Upper assemblage

Two right and two left upper molars and a right lower, L21, belong to a reduncine about the size of a large *Redunca* or small *Kobus*. They are little advanced in the characters of the pinching of the medial lobes of the upper molars and the lateral lobes of the lowers, the outbowing of the ribs between the styles, the complexity of outline of the central cavities, and tendency towards an appearance of anteroposterior compression. Such characters fit a late Pliocene to Pleistocene time level, but it is possible to match them with a minority among dentitions of late Pleistocene and extant reduncines, including *Redunca* cf. *arundinum* from Swartklip (Hendey 1978a: 7). They are, of course, much advanced on the reduncine teeth from 'E' Quarry.

Tribe Hippotragini

Upper assemblage

Four teeth or fragments thereof agree in size and morphology with *Hippotragus gigas* from Elandsfontein. These are left lower molars L1491A and F, a part of an unworn left lower molar L1464J, and part of a left upper molar L1491D. Hendey (1978a: 7) points out that they could also belong to *Oryx gazella*.

Two teeth from the upper assemblage are assignable to *Hippotragus leucophaeus*, the extinct blaauwbok of the southern Cape Province. These are a right M_3 , L2129B, and part of a left lower molar, L2110. The first is in middle wear and has an occlusal length of 28,8 and a height of 19,8. It matches M_3 s of *H. leucophaeus* from Swartklip and Elandsfontein. Such teeth are difficult to distinguish from those of *Kobus* of waterbuck size, although it has to be remembered that for fossils at least back to Upper Pleistocene age in the southern Cape Province *H. leucophaeus* is a more likely identification than a large *Kobus*. Certainly L2129B has a large anterior goat fold and a second basal pillar between its middle and rear lobes, characters which in themselves tell against identification as *Kobus*. A second basal pillar is present in Elandsfontein *H. leucophaeus* SAM-PQ-E3463 and 6323, and in Swartklip SAM-PQ-ZW375, 2254 and 2256A, all of which are from different individuals, and no example of *H. leucophaeus* has been seen in which it is definitely absent. The lower molar L2110 does not give any additional information.

Tribe Alcelaphini

Lower assemblage

A fragmentary right horn-core base with the medial part of its pedicel, L9, belongs to an alcelaphine. It was inserted close to its partner of the other side and the pedicel was higher than in 'E' Quarry alcelaphines. Like *Damalacra neanica*, it was compressed anteroposteriorly, or more accurately, antero-laterally to posteromedially, with a basal index in the region of $37,0 \times 50,0$,

and it curves slightly forward and outward from the base upward. Differences from *D. neanica* are that it may have been inserted less uprightly, its divergence is less, it tapers less rapidly, i.e. it is less thick basally, and the front surface is flatter. The poor divergence is as in *D. acalla*, and this species is a more probable ancestor than *D. neanica*. A flattening of the medial surface near its base may be connected with the lack of divergence of closely inserted horn-cores. This character and the slight outward curvature can be matched within *D. acalla* by L30215. It is almost impossible to guess at a relationship for this form if it were not a Cape descendant of *D. acalla*. Its rather high pedicel could align it with a *Parmularius* species, or the likely course and cross-section of the horn-core could align it with the Hadar Formation alcelaphine and *Damalops palaeindicus*.

L1491E and other alcelaphine teeth from the lower assemblage are of a size to go with L9 and are considerably more advanced than the 'E' Quarry alcelaphine teeth. A larger species is represented by L2112, part of an alcelaphine lower molar rather larger than in living *Connochaetes taurinus*.

Upper assemblage

L1491H is an upper molar of a large alcelaphine of similar size to L2112. Other alcelaphine teeth are from one or more smaller sized species, e.g. L1292, L1373, L1460C, L1464G and K, and L1491B and C.

Tribe Neotragini

Lower assemblage

Some *Raphicerus* horn-cores from Baard's Quarry are smaller than those from 'E' Quarry and small even in comparison with Elandsfontein fossils. They comprise:

L179/7 right $12,6 \times 11,1$

L1645 left $11,2 \times 9,2$

L1663 right $11,4 \times 9,7$

L1670 left $13,8 \times 12,5$, length c. 59,0

Others are L179/6, L905, L906, L1369A, and L1369B

These horn-cores are about the size of those of living *R. campestris*. They are less bulky and do not taper rapidly above the base like those of 'E' Quarry. They are slightly compressed mediolaterally, and their course is more or less straight or with slight forward curvature. L1670 is the most nearly complete and best preserved and it shows an approach to a posterolateral keel. The insertion of L179/7 may be more upright than at Elandsfontein. The postcornual fossa is not as large as in 'E' Quarry horn-cores.

Since the size of *Raphicerus* or *Raphicerus*-like horn-cores declines in the southern Cape from 'E' Quarry to Elandsfontein to extant species, one would imagine that these Baard's Quarry horn-cores came from a time level later than Elandsfontein. They are also small in comparison with the supposed *Raphicerus* horn-core, BPI M 478, from Makapansgat Limeworks. Klein

(1976: 181, figs 2-3) demonstrated size fluctuations of the teeth of Middle and Upper Pleistocene *Raphicerus* in the Cape Biotic Zone, and, if these reflect overall size changes, one can imagine that decline in size has not been steady. However, there is as yet no evidence of *Raphicerus* having such small horn-cores as the Baard's Quarry ones at or before the time level of the Elandsfontein main fauna.

Upper assemblage

Two incomplete horn-cores, L1523 and L1643A, and two unnumbered mandibular fragments are of a size to belong to *Raphicerus*. The latter comprise a fragment of a right mandible with M_2 and part of M_3 , and a fragment of a left with P_4 and part of P_3 . The P_4 has a tendency to transverse orientation of the metaconid as in *Raphicerus*.

The occlusal lengths of the M_2 and P_4 are 10,0 and 7,5 respectively. These may be compared with other samples of *Raphicerus*:

		Number measured	Mean	Range	Standard deviation	Standard error
Recent						
	<i>R. campestris</i> M_2 .	21	9,56	8,7-10,7	0,60	0,13
	P_4 .	21	7,61	7,0-8,5	0,39	0,08
Recent						
	<i>R. melanotis</i> M_2 .	10	8,77	7,8-9,3	0,52	0,16
	P_4 .	10	8,24	7,4-9,3	0,53	0,17
Swartklip						
	<i>R. melanotis</i> M_2 .	9	9,41	8,9-10,0	0,34	0,11
	P_4 .	5	8,06	7,2-9,1	0,68	0,30
Elandsfontein						
	<i>Raphicerus</i> M_2 .	38	10,37	9,0-11,9	0,72	0,12
	P_4 .	16	9,18	8,3-10,1	0,52	0,13

The Baard's Quarry M_2 is within the range of all except the sample of Recent *R. melanotis*, and it is marginally closer to the mean for Elandsfontein than to that for Recent *R. campestris*. The P_4 is within the range of all except the Elandsfontein *Raphicerus* and is closest to the mean of Recent *R. campestris*. It may be that the Baard's Quarry teeth come from Upper Pleistocene or Recent *R. campestris*. According to the findings of Klein (1976: 179), both *R. melanotis* and *campestris* are known in the Cape biotic zone from the earlier Upper Pleistocene onwards, but *R. campestris* occurred with any abundance only at certain times within the Holocene.

Tribe Antilopini

Lower assemblage

The bases of right and left antilopine horn-cores, L179/8 and L179/10, appear to belong to *Antidorcas* since they possess sinuses in their pedicels. The absence of any backward curvature, the oval transverse section and deep

longitudinal grooves on the posterior surface match *A. australis* Hendey & Hendey (1968: 56, pls 3–4) as known from Swartklip and other late Pleistocene sites of the southern Cape Province. The rather small size (basal index = $18,7 \times 16,4$) suggests that the animal would not have been adult. Three teeth are large by comparison with the 'E' Quarry gazelle and could belong to the *Antidorcas*: L179/4C a right M_3 with occlusal length 21,8, L179/4F a right lower molar, and L179/4G part of a left M_3 . The M_3 occlusal length is within the range of both *A. australis* and *A. marsupialis* but is small for the latter species.

Five horn-cores from Baard's Quarry belong to *Gazella*:

L1385B	25,4 × 16,5	L1492	right
L1385C	left 28,0 × c. 19,4	L1521C	right
L1521D	left 26,3 × 19,2		

The last one, L1521D, is the best, or only adequately preserved, one and has a supraorbital pit and a small part of the frontals.

They differ from the gazelle horn-cores of 'E' Quarry by being smaller, more compressed mediolaterally, less curved backward, and the level of the greatest transverse diameter being situated centrally or slightly posteriorly. They agree with the 'E' Quarry form in characters common to many gazelles: a tendency to flattening of the lateral surface, fairly upright insertions in side view, little divergence, and narrowly triangular supraorbital pits. They differ from the Elandsfontein gazelle by being more mediolaterally compressed and more uprightly inserted. Their closest resemblance is to *Gazella praethomsoni* Arambourg (1947) of the Shungura Formation, represented by the holotype in Paris and by three horn-cores from members G and H: L35–35 from G5—a left horn-core with an index of $27,9 \times 18,7$; F516–2 from G27—a right horn-core with index $30,0 \times 20,8$; and F255–73 from H—a right horn-core with index c. $27,5 \times 20,0$. A similar horn-core, BM(NH) M 14508, comes from Bed I at Olduvai Gorge, and has an index of $27,6 \times 21,0$. However, it should be remembered that gazelle horn-cores are not very distinctive, and that a correlation over so long a distance as that from the southern Cape Province to Ethiopia is not very reliable.

AGE OF THE BOVIDAE FROM BAARD'S QUARRY

If one accepts that the fossils from Baard's Quarry come from two distinct assemblages, then the bovids can contribute to assessing their age. The lower assemblage contains a boselaphine not separable, on what we have of it, from the 'E' Quarry *Mesembriportax acrae*, a reduncine which could be as old as 7,0 m.y. yet has teeth, or more correctly a tooth, more advanced than in 'E' Quarry, a *Raphicerus* with horn-cores of a size matched back to the Middle Pleistocene only, an *Antidorcas* apparently akin to the late Pleistocene *A. australis*, and a gazelle different from the 'E' Quarry species. The *Raphicerus* is a problematical species and one needs new provenanced material in order to ascertain that such small horn-cores could be older than the Middle Pleistocene

and so match the date of some of the other fossils. Dental remains apparently of *Raphicerus* occur in the Laetolil Beds and are slightly smaller than extant *R. campestris*, but horn-core or skull remains are as yet unknown. In all it looks as if the lower assemblage is younger than 'E' Quarry but only the *Raphicerus* and *Antidorcas* suggest, or are compatible with, so young an age as the Pleistocene.

The upper assemblage has a reduncine with teeth more advanced than in 'E' Quarry, one hippotragine possibly of Middle Pleistocene age and another of Upper Pleistocene or later age, two alcelaphines with teeth more advanced than those of 'E' Quarry, and a *Raphicerus* with teeth of a size appropriate for Middle Pleistocene or later age. Fauna from the Middle Pleistocene onwards is obviously represented in Baard's Quarry.

DISCUSSION

The Langebaanweg bovids

The 'E' Quarry bovids evidently existed at a time level by which they were sufficiently evolved for their tribal affinities to be clear, but when traces of their shared ancestry were less obliterated than at the present day. Thus the *Tragelaphus* sp., *Mesembriportax acrae*, and *Simatherium demissum* all have horn-cores with fairly wide insertions, some degree of basal divergence and at least one good keel. The last two species also share the characters of strong temporal ridges and a horizontal cranial roof with a rugose surface in its posterior part. Such characters indicate satisfactorily the evolutionary unity of the boodont antelopes. However, it is more difficult to assess the infratribal relationships of the Langebaanweg bovids than of Pleistocene or late Pliocene antelopes. It has therefore been useful to try to assess which character states are primitive and which advanced. It became apparent with the bovine, for example, that *Simatherium* is the only genus with which it can be matched in its supposedly advanced characters of large horn-cores with strong basal divergence and few traces of a (presumed) ancestral shape of cross-section. However, it is important not to lose sight of the subjective and hypothetical element involved in judgements of 'primitive' and 'advanced'. One must also be aware that functional connections within suites of characters may embrace both 'primitive' and 'advanced' characters, as in the bovine *Leptobos*, for example, in which the persistence of the primitively horizontal plane of the braincase roof seems to be linked with the compensatory evolution of very large temporal ridges (Pilgrim 1939: 149). The evidence for paraconid-metaconid fusion on the P₄ of early Reduncini, as discovered during work on the Langebaanweg bovids, is also instructive. One doesn't know if this apparently advanced character should really be taken as primitive for reduncines, whether it is advanced and thus evidence for the view that the 'E' Quarry reduncine is not related to living reduncines (except *Redunca arundinum* ?), or, more elaborately, whether it indicates a character reversal in tooth evolution from early bovids to early

reduncines and then to later reduncines. One cannot have a final opinion on this question.

The bovid species lists for Langebaanweg are:

'E' Quarry

Varswater Formation	QSM	PPM:3aS	PPM:3aN
<i>Tragelaphus</i> spp indet.	O	X	O
<i>Mesembriportax acrae</i>	X	O	X
<i>Simatherium demissum</i> sp. nov.	X	X	X
<i>Kobus subdolos</i> sp. nov.	—	X	X
<i>Kobus</i> sp. 2	—	—	O
<i>Damalacra neanica</i> sp. nov.	—	X	O
<i>Damalacra acalla</i> sp. nov.	O	X	X
<i>Raphicerus paralius</i> sp. nov.	X	X	O
<i>Gazella</i> sp.	O	X	O
Ovibovini gen. et spp indet.	O	O	O

O = rare, X = abundant, — = absent

It is probable that more than one tragelaphine species is present in bed 3aN, and the ovibovine of bed 3aN is definitely different from that of the QSM. Baard's Quarry

Lower assemblage

Mesembriportax acrae
Kobus ?porrecticornis
 Alcelaphini, larger sp.
 Alcelaphini, smaller sp.
Raphicerus sp.
Antidorcas aff. *australis*

Gazella sp., not conspecific with 'E' Quarry species

Upper assemblage

Reduncini sp. indet.
 ? *Hippotragus gigas*
Hippotragus leucophaeus
 Alcelaphini, larger sp.
 Alcelaphini, smaller sp.
Raphicerus sp.

Mesembriportax acrae is the only species common to Baard's and 'E' Quarries, and it is not known whether the alcelaphines or *Raphicerus* are the same in the lower and upper assemblages of Baard's Quarry.

The 'E' Quarry list is not long in comparison with some well-worked sites of later Pliocene or Pleistocene age, e.g. Olduvai Gorge (Gentry & Gentry 1978: 54, table 11) in which any one bed has between twelve and twenty-two species. Since Langebaanweg is a rich locality for mammals as a whole, the relative paucity of bovids probably indicates an antiquity of more than, say, 3 m.y.

There are some indicators of changes in the bovids within the span of the deposits present in 'E' Quarry. Two of the three *Tragelaphus* horn-cores from bed 3aN or probably from 3aN are larger than those from 3aS or, possibly, the QSM. One of them (L40759) differs morphologically as well and probably belongs to a different species. It looks as if the size of *Mesembriportax acrae*, or at least of its teeth, may have increased from the QSM to the PPM. Within the PPM *Damalacra neanica* is more strongly represented in bed 3aS, and

D. acalla horn-cores and an alcelaphine metatarsal reach a larger size in bed 3aN than in 3aS. *Raphicerus* is rare or absent in bed 3aN and the gazelle is also rare there. The supposedly ovibovine cranium from the PPM is very different from that in the QSM. It is possible that reduncine dentitions have larger molars in the PPM than in the QSM and that their horn-cores increase in size between 3aS and 3aN, but neither change can yet be substantiated. Again it is possible that *Damalacra acalla* horn-cores become shorter, the braincase length shortens and the anterior tuberosities of the basioccipital become wider apart, but these differences, too, cannot be substantiated.

Although not rich, the 'E' Quarry bovid fauna appears to be well balanced ecologically. It has one or two species from most tribes, and one cannot see any marked bias in representation comparable with the abundance of Alcelaphini at Olduvai Gorge (Gentry & Gentry 1978: 53, 55) or of Tragelaphini, Reduncini and *Aepyceros* in members B to G of the Shungura Formation (Gentry 1976: 289, tables 2-3). Cephalophini are absent, which is a regular feature of most African fossil localities. So, too, are Hippotragini. Two of the tribes represented, Boselaphini and Ovibovini, are now extinct in Africa and of restricted distribution elsewhere.

Comparisons with other sites

The bovids from one or two east African sites may be compared with those from 'E' Quarry, Langebaanweg. The list for the Laetoli Beds, Laetoli, is:

- Tragelaphus* sp.
- Simatherium kohllarseni*
- Cephalophini sp. indet.
- **Praedamalis deturi*
- *?Hippotragini sp. nov.
- **Parmularius* sp. nov.
- *Alcelaphini sp. indet.
- **Madoqua avifluminis*
- ?*Raphicerus* sp.
- **Gazella janenschi*
- *Sp. indet. aff. *Pelea*

* = common species

The list provides an interesting contrast with Langebaanweg 'E' Quarry in that it has almost the same number of species—11 instead of 12, no boselaphine, 2 hippotragines (the fourth and fifth entries) but no reduncines, 2 alcelaphines of different sizes, and no ovibovine. *Antidorcas* is absent as at Langebaanweg. One can imagine that the ecological bias of Langebaanweg lies towards more closed vegetation and less dry conditions, although the first three species of the Laetoli list indicate that some habitats in which such conditions prevailed must have been present there also.

The Lothagam 1 bovids as listed by Smart (1976: 363) comprise Bosela-

phini 1 species, Tragelaphini 2, Hippotragini 2, Reduncini 2, Alcelaphini 1, *Aepyceros* 1, Neotragini 1, Antilopini 3. There are 13 species here but weaker alcelaphine representation than at Langebaanweg. The Lothagam list also draws attention to the absence of *Aepyceros* at Langebaanweg. The extant impala does not come south of the northern Cape Province, and fossil evidence has yet to be found that it ever did so.

Thomas (1979b) has given a valuable account of the bovids at Mpesida and Lukeino, extending and modifying the preliminary remarks of Gentry (1978a). A *Tragelaphus* as well as *Kobus* aff. *porrecticornis* are known from both these sites. The *Tragelaphus* could be conspecific with the main 'E' Quarry species, unless its horn-cores are insufficiently compressed in the anteroposterior plane, and something close to *Kobus* aff. *porrecticornis* occurs in Baard's Quarry. The absence of a boselaphine at either site and the presence of distinguishable reduncine and tragelaphine teeth are noted by Thomas. A bovine and *Aepyceros* appear at Lukeino, but, apart from *Aepyceros*, no definite Alcelaphini are present at either site. The questionably alcelaphine tooth at Mpesida, KNM-MP 077, of Gentry (1978a: 302) is interpreted by Thomas (1979b, pl. 2 (fig. 11)) as tragelaphine and the questionably alcelaphine horn-core, KNM-MP 068, as being tribe indeterminate (Thomas 1979b, pl. 2, (fig. 12)). The single record for a gazelle or *Raphicerus* is an indication of the difficulty of distinguishing antilopine from neotragine teeth at Mpesida, a situation reminiscent of Langebaanweg.

Faunal correlations

The bovids make some contribution to the problem of correlating Langebaanweg with other sites. One can summarize the conclusions from each species in turn, noting that these conclusions are not always consistent with one another.

The characters whereby the horn-cores of *Tragelaphus* sp. differ from living species of that genus are primitive and suggest considerable antiquity. A similar horn-core is known from Makapansgat Limeworks, while those from Lukeino and the early assemblage of the Kaiso Formation are more primitive and more advanced respectively.

Mesembriportax acrae belongs to a tribe otherwise recorded in Africa from Sahabi, Lothagam 1 (Smart 1976: 363, 365), Ngorora (Gentry 1978a) and Fort Ternan. It is like a large and late *Miotragocerus*, and this could suggest a date somewhat younger than those in the region of 7 to 9 m.y. for Eurasian Turolian sites wherein *M. amalthea* and kindred species occur (Van Couvering & Miller 1971; Erdbrink *et al.* 1976: 98). The most probable age indicated by Smart for Lothagam 1 is a little older than 5 m.y., although the deposits are framed by K-Ar dates of 3.7 and 8.3 m.y. (Behrensmeyer 1976: 166). Ngorora and Fort Ternan are certainly much older and the age of Sahabi is as yet conjectural. Thus, somewhere about 5.5 m.y. is a likely age for the latest known boselaphine in Africa. Boselaphini become rare or locally extinct everywhere after the Turolian or equivalent stages. In Pakistan *Miotragocerus* disappears

towards the top of the Dhok Pathan Formation at a level where Reduncini make their first appearance (Pilbeam *et al.* 1977: 687), perhaps about 7,5 m.y.

Simatherium demissum is less advanced than the *Simatherium* in the Laetolil Beds, so may be older than 3,5–3,75 m.y. The bovine *Parabos boodon*, which is at a comparable evolutionary level on a different lineage, comes from Perpignan, which is given an age of about 4,8 m.y. by Berggren & Van Couvering (1974: 92, fig. 11) and Delson (1975). The earliest bovine fossils yet known in Africa are the Lukeino teeth which Thomas (1979b) assigned to *Ugandax*. In the Siwaliks Group, Bovini first appear in the Tatrot stage.

The temporal lines on the braincase roof of *Kobus subdolus* are much weaker than in Pinjor Formation reduncines and no close relationship with these animals is likely. *Kobus subdolus* horn-cores are not like those of either *K. porrecticornis* or *K. aff. porrecticornis* from the Tatrot and/or upper Dhok Pathan Formations, Lukeino, Mpesida, and the Amado Formation, Afar. The teeth which seem to belong to *K. subdolus* are unlike any other known reduncines including the *K. porrecticornis* stock, so either 'E' Quarry is older than about 7 m.y. or one has to suppose that *K. subdolus* retained primitive teeth longer than did the smaller *K. porrecticornis*. The horn-cores of *K. subdolus* do have similarities to others from Sahabi and Wadi Natrun, but as yet no reduncine teeth are known from these sites.

Kobus sp. 2 looks more like an earlier member of the kob lineage than the species found in member B of the Shungura Formation, but this appearance may be a misleading parallel. It has an interesting conformation of its frontals which could well be primitive, as already suggested.

The small *Kobus* of Baard's Quarry does not occur in 'E' Quarry but appears to be very close to *K. porrecticornis* and *K. aff. porrecticornis*. It is kob-like and may be related to later reduncines.

The alcelaphines of Langebaanweg support the age interpretations arising from consideration of the reduncines. It is difficult to relate them to east African fossil alcelaphines, but a much damaged horn-core, an upper molar, and an M_3 from Wadi Natrun look as if they could be similar. Alcelaphine teeth at Langebaanweg are markedly more primitive than those known from either the Hadar Formation or the Laetolil Beds and are much less hypsodont than at the Sterkfontein Type Site. They are more advanced than teeth of *?Pseudotragus* in the Ngorora Formation which may belong to a species ancestral to later Alcelaphini.

The horn-cores of *Raphicerus paralius* are similar to one from Makapansgat Limeworks. A pair from member G of the Shungura Formation have some similarities to *R. paralius*, but neotragine dentitions in member G are dissimilar. *Raphicerus paralius* is the largest known neotragine and appears to be much older than the *Raphicerus* from Elandsfontein. Neotragine dentitions at Langebaanweg are at so early an evolutionary level that it is difficult to tell them from dentitions of Antilopini. The same difficulty is found at Mpesida.

If it were accepted that the Langebaanweg gazelle was ancestral to the one from Makapansgat Limeworks, it would follow that Langebaanweg was an

older site.

The ovibovine is likely to be older than those from Makapansgat Lime-works and the Hadar Formation, mainly on the indication of the primitive state of its basioccipital. It is definitely not a member of the Turolian-aged group of ovibovines centred on *Urmiatherium*.

Conclusions

Sahabi is perhaps the site with bovids most akin to Langebaanweg. It has a boselaphine of Turolian aspect coexisting with a primitive bovine as at Langebaanweg, and its reduncine horn-cores, too, are similar to those of Langebaanweg. One is uncertain without the benefit of K-Ar dating whether to rely on the boselaphine and favour a date back to somewhere near 7-8 m.y. for both sites, or to emphasize the affinities of the bovines with their more advanced relatives in middle and late Pliocene faunas and thus favour a date nearer to 4 m.y. Sahabi has generally been allotted to a position about 6 m.y. (Maglio 1973: 70) or 6.5 m.y. (Delson 1975).

The *Kobus* aff. *porrecticornis* at Mpesida and Lukeino suggests that these sites could be younger than 'E' Quarry, but the *Tragelaphus* suggests, less forcefully, that Lukeino could be older. The neotragine or antilopine dentitions suggest that Mpesida could be about the same age as 'E' Quarry.

The reduncine and alcelaphine teeth at Langebaanweg favour an early date, perhaps even earlier than 7 m.y. in the case of the reduncines. However, securely dated alcelaphine teeth of 'advanced' pattern are not known earlier than from Laetoli (3.5-3.75 m.y.), and one can envisage that alcelaphine teeth may have evolved at an accelerated rate, i.e. crossed a threshold, shortly before this time. With a site in the extreme south of Africa there is always the possibility that evolutionary advances lagged behind those in other parts of Africa. At the present time the teeth of *Connochaetes gnou* and *Damaliscus dorcas* are less occlusally complex than in other living alcelaphines. Allometry may be involved in either case and especially in *D. dorcas*, but it is also possible that *C. gnou* has retained a primitive condition. However, it would be unwise to introduce the idea of a South African evolutionary lag into palaeontological correlations in the absence of evidence of its independence from allometric effects or of its persistence over a period of several hundred thousand years.

As a whole one can say that the bovids best indicate an age of about 6 m.y. for the fauna of 'E' Quarry at Langebaanweg, near the end of the Turolian Stage in Europe, and near the base of the Tatrot Formation in India and Pakistan. The bovids of the lower assemblage in Baard's Quarry suggest a pre-Pleistocene age younger than 'E' Quarry, and the upper assemblage a Middle Pleistocene or later age.

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